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UNIVERSITY OF ALBERTA

Bioenergetics and trophic relationships of Arctic cod (*Boreogadus saida*) in the Canadian High Arctic

by

Haakon Hop

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements
for the degree of DOCTOR OF PHILOSOPHY.

Department of Zoology

EDMONTON, ALBERTA

SPRING 1994

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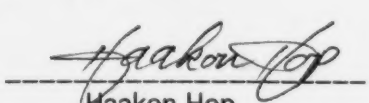

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DEDICATION

To anyone with "Arctic dreams"

Abstract

Bioenergetics and feeding ecology of Arctic cod (Boreogadus saida) were studied at low ambient temperatures, close to 0 °C. The feeding ecology of adult Arctic cod depended upon schooling behavior; schooling fish were not successful in terms of feeding (64.6 % empty stomachs), whereas dispersed fish fed extensively on arctic amphipods and copepods. The gonadosomatic index was 3-4 % at the time of schooling (August-September), and increased to 47.7 % for females and 22.3 % for males at spawning time (mid February). Potential fecundity averaged 26,500 eggs, rich in phospholipids, having a mean diameter of 1.6 mm. Levels of sex steroids in gonads of ripe females were much lower than those of unripe fish. Most of the energy for gonadal development came from triglyceride stores in the large liver.

Arctic cod spent relatively little energy for maintenance at low temperatures, although oxygen consumption rates (VO_2) increased rapidly with temperature (Q_{10} = 7, for a 2.3 °C temperature increase). Respiration depended on acclimation time to holding conditions, with fish acclimated for 5 months having a much lower VO_2 (46.56 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$) than short-term acclimated fish (88.71 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$). Feeding to satiation increased VO_2 values by 32-62 % above pre-fed values.

Maximum daily rations for Arctic cod were low both for juvenile (99-168 mg $\cdot d^{-1}$) and adult fish (408-647 mg $\cdot d^{-1}$). Slow digestion rates at low temperatures may limit daily food intake when food is abundant, since it took up to two weeks for fish to fully evacuate stomachs. Maintenance rations (74 mg $\cdot d^{-1}$ or 0.6 % body weight $\cdot d^{-1}$ for small fish) reflected the low energy requirements for respiration. Based on measurements of consumption (C), growth (G), respiration (R), egestion (F), and excretion (U), an average energy budget for juvenile Arctic cod feeding on zooplankton was :
100 C = 50 G + 33 R + 3 F + 6 U + 8 Z, where Z included activity and energy unaccounted for. Because of low consumption rates, growth rates were slow

(38-63 mg · d^{-1} or 0.6-1.5 % body weight · d^{-1} for small fish), although assimilation efficiencies were high (about 80 %) as were gross and net growth efficiencies (50 and 60 %, respectively).

The key role of Arctic cod in the high arctic marine food web, as the dominant prey of several seabird and marine mammal species, is predominately a result of their high standing biomass, which subsequently leads to high annual production despite the slow growth of individual fish.

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CHAPTER 1

General introduction:

The Arctic cod (Boreogadus saida) and its function in the high arctic marine food web

General introduction

The Arctic cod (Boreogadus saida Lepechin, 1774) is the only member of its genus in the family Gadidae (Rafinesque, 1810) (Cohen et al. 1990). Some of its distinguishing features are: slender body, projecting lower jaw, reduced barbel, forked caudal peduncle, moderately large pectorals and small pelvics with the second fin ray extending well beyond the range of the other rays. The color is usually dark brown to black above and silvery below, but speckled and silvery colored individuals occur. It is a small fish (maximum length 320 mm; Leim and Scott 1966), short lived (maximum age 7 years; Bradstreet et al. 1986), matures early (males at age-2 and females at age-3; Craig et al. 1982), and spawns in winter beneath the ice, with peak spawning between January and February in Russian waters (Andriyashev 1954).

The Arctic cod has a circumpolar distribution mainly above the Arctic circle (Svetividov 1948; Andriyashev et al. 1980; Cohen et al. 1990) and is probably one of the most abundant fishes in the Arctic (Moskalenko 1964; Ponomarenko 1968). Its southern distribution, in the western North Atlantic, is limited to cold waters off the coasts of Northern Labrador and Newfoundland (Lear 1979; Scott and Scott 1988).

Although comparatively little is known about the detailed aspects of high arctic marine food webs and specific rates of energy transfers between trophic levels, there is little doubt that a considerable fraction of the annual energy flow passes through Arctic cod (Hobson and Welch 1992 a; Welch et al. 1992). The energy flow model of Welch et al. (1992) sums up what is presently known about the energy flow for parts of the marine food web in the Lancaster Sound region, N.W.T., and Hobson and Welch (1992 a) used stable isotope analysis to determine trophic relationships within this food web. Both studies identified the Arctic cod as a key component of the high arctic marine food web, since it transforms the energy of small invertebrates into packets large enough to be exploited by higher trophic levels. The large biomass of Arctic cod is then a

major food source of several marine mammals, particularly ringed seals (Phoca hispida), harp seals (Phoca groenlandicus), narwhal (Monodon monoceros) and beluga (Dephinapterus leucas), as well as sea birds, such as Thick-billed murres (Uria lomvia), Northern fulmars (Fulmarus glacialis), Black-legged kittiwakes (Rissa tridactyla), Black guillemots (Cepphus grylle), and to some extent Arctic terns (Sterna paradisaea) (Bradstreet 1980, 1982; Davis et al. 1980; Bradstreet and Cross 1982; Bradstreet et al. 1986; Hobson and Welch 1992 a, b; Welch et al. 1992; Welch et al. 1993). The Arctic cod is not commercially exploited in Canada, but has been exploited as an industrial fish, for fish meal and oil, in the Barents Sea (Gjøsæter 1973; Filippov 1974; Falk-Petersen et al. 1986). Reviews of the general biology of Arctic cod include works by Klumov (1937), Andriyashev (1954), Moskalenko (1964), Leim and Scott (1966), Hognestad (1968), Bain and Sekerak (1978), Sameoto (1984), Bradstreet et al. (1986), Scott and Scott (1988), and bibliographies are covered by Bradsteet et al. (1976), Dewar et al. (1983), and Sameoto (1984).

Despite the importance of Arctic cod within the arctic marine food web, relatively little is known about the bioenergetics of this species, apart from the studies by Jensen et al. (1991) on controlled feeding and growth, and by Holeton (1974) on respiration. Experimental work has mainly focused on artificial fertilization and embryonic and larval development (Doroshev and Aronovic 1974; Aronovic et al. 1975; Althukov 1981). The only complete energy budget that exists for a polar fish species is that of Everson (1970) for the Antarctic icefish (Notothenia neglecta Nybelin, 1951), whereas none exist for arctic marine fishes. However, many field studies have investigated the distribution, feeding ecology and various life history aspects of Arctic cod (e.g., Barenkova et al. 1966; Ponomarenko 1967, 1968; Rass 1968; Lowry and Frost 1981; Craig et al. 1982; Moulton and Tarbox 1987; Lønne and Gulliksen 1989; Crawford and Jorgenson 1993).

This doctoral thesis investigates the bioenergetics and trophic relationships of Arctic cod in the Canadian High Arctic. It is the first

dissertation on this fish species, and the first to present a complete energy budget for an arctic marine fish. The thesis includes information on feeding ecology and population structure of Arctic cod in the wild, although its main contribution is through an experimental approach to feeding energetics at low temperatures. The objective was to quantitatively evaluate the feeding ecology and bioenergetics of Arctic cod, and the importance of this species to higher trophic levels in the high arctic marine food web.

The first data chapter (Chapter 2) is an ecological study of the population structure and feeding ecology of Arctic cod, especially schooling fish, which are behaviorally different from non-schooling or dispersed individuals. This chapter complements a study (Welch et al. 1993) that showed that Arctic cod schools may be subject to intense predation pressure by sea birds and marine mammals, particularly by beluga whales.

The next three chapters include various aspects of bioenergetics of Arctic cod. Chapter 3 quantifies respiration and how respiration is affected by acclimation, temperature and feeding. Chapter 4 is a study of spawning energetics, including potential fecundity and energy lost during spawning, and also provides information on seasonal development of the ovary and plasma sex steroids. It complements a recent study by Graham and Hop (in prep.) on aspects of reproduction and larval biology of Arctic cod from Canadian arctic waters. Chapter 5 then deals with one aspect of feeding energetics, investigating gastric evacuation rates and daily rations.

Chapter 6 treats feeding energetics more thoroughly, based on experiments with individuals and groups of Arctic cod fed different diets and rations. Information on feeding, growth, respiration and waste losses is incorporated into an energy budget for the species. Therefore, this chapter also partly serves as a general discussion of bioenergetics of Arctic cod. Implications of the results for the ecology and bioenergetics of Arctic cod are discussed in Chapter 7, and some general conclusions are drawn. Finally Appendix 1 presents a method for quantifying the energy of stomach contents

from arctic seabirds, and gives some preliminary results on the energy contribution of different prey groups to seabird diets.

This project has resulted partly because of increased interest in Arctic cod in connection with marine mammal research/management and resource exploitation in the Canadian High Arctic (e.g., Davis et al. 1980). Increased exploitation of arctic resources may eventually alter arctic ecosystems and subsequently alter energy flow in food chains, such as has been observed in the North Sea and the Barents Sea after the collapse of herring (Clupea harengus L.) and capelin (Mallotus villosus Müller, 1777) stocks (e.g., Vader et al. 1989; Vader et al. 1990). To understand, model and predict effects of man-induced alterations on the energy flow through arctic food webs, one first requires the energy budgets of individual components in unaltered systems, particularly the important ones such as Arctic cod in the high arctic marine food web. Thus, this study contributes to this knowledge by solving the energy budget for one important component of the third trophic level of the high arctic marine food web.

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CHAPTER 2

Population structure and feeding ecology of Arctic cod (*Boreogadus saida*) schools in the Canadian High Arctic

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Introduction

Schools of Arctic cod (Boreogadus saida Lepechin, 1774) occur throughout the circumpolar range of the species, and have been observed in Canadian (Bain and Sekerak 1978; Welch et al. 1992; Welch et al. 1993), Greenlandic (Welch et al. 1993), Alaskan (Craig et al. 1982) and Russian waters (Ponomarenko 1967, 1968; Rass 1968). In addition, non-schooling or scattered individuals are present during both the ice-covered and open-water seasons.

Bain and Sekerak (1978) recorded mass movements of Arctic cod (size range 110-240 mm) into Allen Bay, Cornwallis Island, N.W.T., in July-September, and Crawford and Jorgenson (1993) observed that schooling density was negatively related to the amount of drifting ice cover. Craig et al. (1982) sampled both juvenile and adult schools in Simpson Lagoon, Alaska, and such schools have also been sampled in Russian waters (Moskalenko 1964; Andriyashev et al. 1980). However, due to the unpredictable and often ephemeral occurrences of Arctic cod schools, they are not frequently sampled and relatively little is known about their population structure or feeding ecology. Arctic cod generally feed pelagically on copepods and amphipods, on ice-associated amphipods and on epibenthic crustacea (Bradstreet et al. 1986; Lønne and Gulliksen 1989). This species is a central component of the arctic marine food web (Klumov 1937; Hobson and Welch 1992; Welch et al. 1992), and schools may be subject to intense predation pressure by seabirds and marine mammals (Welch et al. 1993). In this paper we investigate ecological aspects of schooling Arctic cod, and make comparisons, where possible, between juvenile and adult schools and with non-schooling cod.

Materials and Methods

Samples from Arctic cod schools were obtained during July-September, 1985-91, from Resolute and Allen Bays on Cornwallis Island, Gascoyne Inlet,

Erebus and Radstock Bays on the southwest coast of Devon Island, and Grise Fiord on southern Ellesmere Island (Figure 2-1). We determined the temperature profile daily at one of these locations, Resolute Bay (5 km^2, maximum depth 29 m with a 10-15 m deep sill at the mouth), from mid-July to mid-September, 1989. The other bays/inlets range in size from 15 km^2 (Gascoyne Inlet) to 200 km^2 (Radstock Bay), with the largest bays deepening to 150 m.

Sampling was opportunistic, and employed three types of trawl (bottom, Kuichak and Isaacs-Kidd), trap nets, gill nets, dip nets and a cast net. The bottom trawl was a small otter trawl with a 4.9 m head rope, 5.1 cm mesh netting, and a 3.8 cm mesh cod end with a 1.3 cm mesh inner liner. The Kuichak midwater trawl had a 7.5 m^2 aperture, with 3.8 cm mesh netting grading down to a 0.6 cm mesh at the cod end, and was rigged with spreader bars connected to a bridle to maintain its mouth opening. Because it could not be towed fast enough to effectively catch adult fish, it was dropped onto a school in relatively shallow water by tossing it from the boat. The Isaacs-Kidd midwater trawl had a 2.2 m^2 aperture with a 6.4 cm mesh body, a 1.3 cm mesh inner liner and a 0.3 cm mesh cod end. Schools were also caught in trap nets (8 m^3 box, 6 m wings, 20 m lead), set overnight perpendicular to shore, with the leads in < 2 m of water and the box at 5-8 m depth. The presence of schools was indicated by overnight catches of > 5,000 individuals, compared with regular catches of < 500 fish. Other sampling gear included sinking experimental gill nets (1.8 m height, with six 13.7 m long panels of 20, 37, 65, 90, 110, 120 mm stretched mesh), dip nets, and a cast net (4.3 m diameter, 0.95 cm mesh).

Fish were weighed whole (TW, g) and fork length was measured (FL, mm). Specimens measured as total length (TL, mm) were converted to fork length: $FL = (TL + 2.008) \cdot 0.9515$ ($r^2 = 0.998$, n = 55, range 70-210 mm). We determined Fulton's condition factor, $C = (TW \cdot 10^5) \cdot FL^{-3}$ (Ricker 1975), and age was determined from cross-sectioned otoliths (Chilton and Beamish 1982).

Gonads were dissected out, weighed wet (GW, g), and sexed by external morphology (Vladykov 1972; Lear 1980). Gonadosomatic index, $GSI = (GW \cdot TW^{-1}) \cdot 100$, where GW and TW are gonad weight and whole body weight, respectively.

Stomachs were removed and the apparent degree of stomach fullness was determined on a scale from 1-5: (1) Empty, (2) < 1/3 full, (3) 1/3-2/3 full, (4) > 2/3 full, (5) completely full and distended. Total blotted wet weight of stomach contents was expressed as a percentage of total fish weight.

To assess whether large schools of Arctic cod might deplete zooplankton food sources locally, we sampled zooplankton at several locations in 1990: in Allen Bay near where fish were schooling, at two adjacent sites within Allen Bay, at a neighboring bay (Resolute Bay), and off-shore in Resolute Passage. Vertical plankton tows were taken from maximum depth or 30 m, whichever was least, using paired 0.5 m diameter bongo nets of 1 mm mesh. Of all zooplankton collected only Calanus hyperboreus and C. glacialis were present in sufficient numbers to analyze. They were sorted to stage and grouped as "large" (3.3-4.4 mm body length, which included C. hyperboreus IV-VI plus C. glacialis V-VI) and "small" (1.9-2.5 mm, which included C. hyperboreus III plus C. glacialis III-IV).

Results

Environmental conditions and school occurrences

Thermal conditions in Resolute Bay were relatively stable, varying about ± 1.5 °C annually. From October to mid-June water temperature is < -1.5 °C, the water column being almost isothermal at -1.8 °C from March to June (Bergmann 1989). Ice break-up usually occurs in late July, and after that surface waters warm up slightly and may reach a maximum of 1.0 °C (Figure 2-2). Increasing winds in September mix the water column and subsequent surface cooling lowers the temperature to about -1.5 °C before freeze-up.

Juvenile Arctic cod schools were observed in Resolute Bay in July (Table 2-1), corresponding with the early warming of surface waters. In 1989 these schools occurred in shallow water under the ice, and individuals were frequently observed in ice cracks, or even swimming in brackish water on the ice. Elsewhere we observed juvenile Arctic cod in brackish meltwater and frequently caught them near river mouths.

Adult schools were observed from late-July to mid-September, most frequently in August (Table 2-1). Most schools in the bays of Cornwallis and Devon Islands occurred in relatively shallow waters during the warm period. For example, at Gascoyne Inlet in August, 1985, schools were observed in shallow (< 5 m) waters at a temperature of about 2 °C (Bergmann 1989). However, schools have also been detected hydroacoustically in deeper (< 25 m) water in Allen Bay (Welch et al. 1993). Shallow water schooling events normally attract feeding seabirds and marine mammals; indeed, marine mammals may have driven some schools into the shallow regions (Welch et al. 1993).

Size structure of schools

Mean sizes of fish in adult schools were 138-207 mm FL (Table 2-1), with the overall size ranges being 110-260 mm. Length distributions varied among areas and gear (Figure 2-3 a-d), although some similarities were apparent. Length distributions from gill and trap nets in Resolute Bay were similar when small fish (< 100 mm) were excluded from the trap net catch (Kolmogorov-Smirnov test, $p > 0.05$; Figure 2-3a). Also, length distributions of three trawl samples from Allen Bay (1989, 1990), with the bottom trawl towed through the school in mid water, did not differ significantly (K-S, $p > 0.05$; Figure 2-3b). Length distributions may vary between areas since fish caught in Allen Bay were smaller (Kruskal-Wallis test, $p < 0.05$) than those caught in Resolute Bay (Kruskal-Wallis test, $p < 0.05$), and fish caught with the same bottom trawl in Gascoyne Inlet (1988) had a significantly different length

distribution (K-S, $p < 0.05$) than those caught in Allen Bay, although their mean length was similar (Table 2-1). When data were pooled among years in Allan Bay, it became apparent that different gear (trap net, bottom trawl and Isaacs-Kidd trawl) caught different length distributions of fish (K-S, $p < 0.05$; Figure 2-3c). The beach-stranded fish from Grise Fiord also had a different distribution, skewed towards larger fish, possibly because seabirds had eaten the smaller ones (Figure 2-3d).

Juvenile schools from Resolute Bay consisted of fish that ranged from 65-105 mm (Figure 2-3e). Non-schooling cod, caught in a trap net and bottom trawl in Resolute Bay, consisted of all sizes > 50 mm (Figure 2-3f).

Age distribution

Arctic cod are slow growing, reaching a mean length of 224 mm at age-7 (Figure 2-4a), with the largest schooling individual being 268 mm. Adult schools consisted of age-classes 2-7, with ages 3-4 being dominant (overall mean 3.7), whereas juvenile schools consisted mostly (> 90 %) of age-1 fish (Figure 2-4b). There were generally no significant differences in age distributions among samples (pooled for years) from different areas (K-W, $p > 0.05$), or between years in Allen Bay ($p > 0.05$). One exception was a trap net sample from Allen Bay (1989) with unusually large fish (Table 2-1) of mean age 5.1. Age-class 2 was nearly absent from both juvenile and adult schools, and was infrequently caught outside schools. Non-schooling fish included both age-1 and older fish (mostly ages 4-5), with age-3 fish being underrepresented.

Feeding ecology and condition factor

Adult schools were composed of fish that were generally not feeding, or only feeding occasionally (Figure 2-5a). They had a high frequency of empty stomachs, 64.6 % on average, compared with 5.5 % for non-schooling adults (Table 2-2; Figure 2-5b). For example, the 1990 Allen Bay school had empty stomachs on 8 August. On 15 August 55.4 % of the fish had evidence of food in

their stomachs. Then, on 28 August most of the stomachs (99.0 %) were again empty (Figure 2-5a). Juveniles, schooling or not, had low frequencies (< 10 %) of empty stomachs (Table 2-2). Both juveniles and non-schooling adults frequently had full to extremely full stomachs (Figure 2-5b).

Schooling fish had significantly lower condition factors than non-schooling individuals, when samples were pooled among years (two-tailed t-test, $p = 0.0261$) (Table 2-1). The mean condition factor (C) for a subsample (those of Table 2-2), in which with stomach weights were subtracted, remained lower for schooling ($C = 0.688$) than non-schooling fish ($C = 0.734$), which is equivalent to a 6 % weight loss, although the difference was not statistically significant ($p = 0.1064$).

The most abundant food items in stomachs of schooling adults were the pelagic hyperiid amphipod Parathemisto libellula and large Calanus copepods. Juvenile fish, in schools or not, fed almost exclusively on calanoid copepods, but also took cyclopoid and harpacticoid copepods. Non-schooling adults fed on Calanus (C. hyperboreus, C. glacialis), amphipods (genera Parathemisto, Onisimus, Gammarus, Gammaracanthus, Monoculodes, Weyprechtia, Paroediceros, and Apherusa), and epibenthic crustacea (Mysis spp.) (H. Hop, unpubl. data).

Even the occasional feeding of large schools may temporarily deplete planktonic prey populations in their local area. When a large school was present in one of the inner basins of Allen Bay in 1990 (location A, Figure 2-6), the proportion of large Calanus was reduced, as compared with other sites examined (locations B-E, Figure 2-6). Samples from this school on 15 August indicated feeding (Table 2-2), and large copepods were relatively depleted at this location on 21 August. Subsequently, the school had empty stomachs on 28 August (Table 2-2), and plankton sampling on 4-6 and 12-15 September showed no depletion of large Calanus relative to Resolute Bay (Figure 2-6).

Sex ratio and gonad development

The mean sex ratio (males/females) of schooling fish samples was 0.85 (range 0.55 to 1.23; Table 2-4), indicating a slight but significant surplus of females (Binomial test, $p = 0.0163$). Males (mean FL = 155 mm) were somewhat smaller than females (166 mm). A higher proportion of the small fish were males and a higher proportion of the large fish females, although the overall length distributions were not significantly different (K-S, $p = 0.4927$). The overall sex ratio for non-schooling fish (0.95; Table 2-4) was not significantly different from a 1:1 ratio ($p > 0.05$).

Male gonad development for schooling Arctic cod starts in August (Figure 2-7). Female gonads start rapid development later (October/November), and reach full development in February, 1-2 months after males (H. Hop and M. Graham, unpubl. data). Gonads are therefore not well developed during the period reported here, with gonadosomatic indices of 2.4-5.6 % for males (mean 3.8 %) and 2.1-3.4 for females (mean 2.8 %) (Table 2-4), representing 13 % and 6 % of ripe GSI for males and females, respectively (H. Hop and M. Graham, unpubl. data).

Discussion

Arctic cod typically aggregate annually in the shallows at various locations of the eastern Canadian Arctic during a specific time window of about two months (Welch et al. 1993), although a portion of the population is dispersed at the same time. We identified two types of Arctic cod schools having different age structures and feeding ecologies: non-feeding schools of mostly adults and actively feeding juvenile schools.

Observed schooling occurrences may partly reflect seasonal variation in observational efforts as a result of ice conditions. We observed schools from July-September, whereas other researchers have observed schools in winter as

well (Moskalenko 1964; Andriyashev et al. 1980); however, it appears that fish disperse after spawning (Moskalenko 1964).

Little is known about the reasons for the inshore schooling behavior of Arctic cod, and environmental or biological factors may affect adult and juvenile schools differently. Responses to temperature (Hognestad 1968; Craig et al. 1982), food resources (Craig et al. 1982) and predators (Crawford and Jorgenson 1993; Welch et al. 1993) have been suggested as potential causes of schooling.

Juvenile schools occurred in July in association with ice in warming shallow waters. These fish may have been attracted to the slightly warmer surface waters during this time of the year, but also to the abundant food resources associated with the ice pack, since they fed heavily on copepods at the time.

Adult schools occurred in inshore waters later (August-September). This corresponded to a 1.5°C temperature increase in the upper 10 m of the water column, but schools were also observed in deeper water where the temperature was < 0 °C. Schooling behavior may be a response to temperature prior to spawning (Sameoto 1984), implying that increased temperature would influence gonad development. Our observations indicated that male gonads start developing at the time of schooling in August, whereas female gonads showed little development, and spawning does not occur until late winter (Barenkova et al. 1966; Ponomarenko 1967; Craig et al. 1982).

Adults schools are often observed in association with aggregations of marine mammals and seabirds exploiting this temporarily abundant food resource (Finley et al. 1980; Welch et al. 1993). Even though predators may not cause schools to form (Welch et al. 1993), mass strandings, such as the one in Grise Fiord and others reported in Allen Bay (Bain and Sekerak 1978; Welch et al. 1993), are probably often induced by predators forcing fish into shallow water (Welch et al. 1993). However, mass strandings have also been observed

after severe storms in Alaskan and Russian waters (Klumov 1937; Shibanoff 1958; Moskalenko 1964; Craig et al. 1982).

Ages 3-4 were the dominant year-classes in adult schools; these represent adult fish since most Arctic cod are mature at age-2 to 3 (Craig et al. 1982). Age-distributions will depend somewhat on gear selectivity, but dominant year-classes were likely correctly represented since these same ones have also been detected in other studies (e.g., Moskalenko 1964). Age distributions varied little among locations and date, and there was no evidence of a cohort dominating from one year to the next in Allen Bay. Probably because age-3 fish were abundant in schools, this year-class was underrepresented in non-schooling samples. Length distributions of schools were also similar over time within an area, although they varied between areas. It is unknown whether Arctic cod in the study areas belong to the same population, but assuming that they do, some of the variation between areas may have resulted from gear selectivity.

Age-2 fish did not appear to any extent in either juvenile or adult schools, and may therefore have moved elsewhere. Fish schools, most likely Arctic cod, have been detected hydroacoustically in Canadian arctic waters deeper than 100 m (R.E. Crawford, unpubl. data), but it was unknown whether these aggregations included this year-class. In offshore catches from the western coast of Alaska, the most abundant year-class was age-2 (Wolotira et al. 1979). The age-0 year-class, common in the waters of our study area, are planktonic (Barenkova et al. 1966) and not vulnerable to the gear we used.

The overall sex ratio in adult schools indicated a slight surplus of females, although a higher proportion of the small fish were males. Males grow slightly faster than females (Wolotira et al. 1979), and a higher fraction of males reaches maturity earlier (age-2) than females (Craig et al. 1982). Since this study, as well as others (e.g., Moskalenko 1964; Wolotira et al. 1979; Craig et al. 1982), found that a higher proportion of the large fish in samples were females, it is likely that the mortality rates are higher for males than females.

Although the juvenile schools seemed to be feeding aggregations, there was no similar evidence for adult schools. Instead our data suggested that adult Arctic cod exhibit two distinct behavioral strategies during this time of the year: participate in schools and generally forego feeding, or disperse individually to feed. It is not known whether non-schooling fish will join schools for periods of time or whether schooling fish will leave temporarily to feed (Bradstreet et al. 1986). Schools have been observed periodically at the same general location in Allen Bay for up to two months (Welch et al. 1993). High frequencies of empty stomachs (90-100%) indicate that individuals are not returning to the schools after feeding, and individuals with empty stomachs must have been starving for at least two weeks because of slow gastric evacuation rates (H. Hop and W.M. Tonn, unpubl. data). However, the occasional feeding by fish in large schools may be sufficient to deplete zooplankton locally, as exemplified by the low ratio of large:small copepods in the vicinity of the Allen Bay school in August 1990. It is unlikely that fish school because of low food supply since there was no evidence of resource depletion in Allen Bay in September 1990.

In contrast, non-schooling individuals fed extensively on copepods, amphipods and mysids, and a high frequency of full to extremely full stomachs suggested that they fed almost continuously during July-September.

There appeared to be an energetic cost of schooling for adults since schools occurred at a time when food resources were generally abundant, but schools did do not move to nearby resource rich areas after their local area became depleted. The absence of feeding was reflected in the lower condition factors of schooling fish, although the difference was not significant when adjusted for stomach weight, possibly because of low sample size of non-schooling fish. However, any energetic cost, as measured by condition factor, would be minor since fasting Arctic cod lose < 10 % of their body weight per month at low ambient temperatures (H. Hop and M. Graham, unpubl. data), and with a high assimilation efficiency (about 0.80), this loss may be reduced

substantially if they feed occasionally. The small reduction in condition factor suggested weight loss of about 6 %, but most samples had been collected within only three weeks of the first recorded schooling events (end of July). Any energetic costs of schooling are apparently outweighed by benefits, such as predator protection.

Table 2-1. Sampling date, gear, and means (± SE) of fork length (FL), weight, and condition factor (CF) of samples from adult and juvenile Arctic cod schools, and non-schooling cod, 1985-91. Group means (± SE) are calculated from the means of individual collections.

Location	Date (d/mo/yr)	Gear	n	Mean FL (mm)	n	Mean wt. (g)	CF (x 1000)
ADULT SCHOOLS							
Resolute Bay	21/8/86	Gill net	93	184.4±2.0	93	48.1±1.4	752±7
Resolute Bay	31/7/88	Trap net	511	173.7±1.4	195	-	794±7
Allen Bay	26-27/7/89	Trap net	108	206.8±2.0	42	69.5±4.1	736±11
Allen Bay	2/9/89	Bott.trawl [a]	101	146.1±2.8	101	23.0±1.8	655±5
Allen Bay	16/9/89	Bott.trawl [a]	99	148.1±2.3	99	24.1±1.3	699±7
Allen Bay	8/8/90	Trap net	100	146.8±2.2	100	23.5±1.1	707±7
Allen Bay	15/8/90	Bott.trawl [a]	201	151.2±1.8	101	28.9±1.6	730±11
Allen Bay	28/8/90	Isaacs-Kidd tr.	400	176.3±1.5	200	43.0±1.7	678±5
Gascoyne Inlet	8/8/85	Hand caught	79	179.1±2.4	79	34.2±1.4	576±8
Gascoyne Inlet	23/8/85	Kuichak trawl	967	168.6±0.7	190	33.7±0.1	656±0
Gascoyne Inlet	18/8/88	Bott.trawl [a]	178	148.8±1.3	178	22.4±0.6	654±5
Erebus Bay	19/8/88	Dip net	89	166.5±2.0	89	33.3±1.2	698±6
Radstock Bay	31/7/91	Cast net	100	138.2±1.5	97	18.7±0.7	716±7
Grise Fiord	16/9/87	Beach stranded	47	178.8±4.4	47	48.2±3.5	783±12
Group mean (± SE)			14	165.2±5.2	14	34.7±4.0	702±15
JUVENILE SCHOOLS							
Resolute Bay	14,20/7/89	Dip net	50	85.4±0.9	50	4.2±0.2	657±8
Resolute Bay	31/7/91	Bott.trawl [b]	100	79.6±0.6	40	3.1±0.1	661±8
Group mean (± SE)			2	82.5±2.9	2	3.7±0.5	659±2
NON-SCHOOL ADULTS							
Resolute Bay	9,26/8/85	Bott.trawl [b]	34	140.2±5.6	34	27.8±3.8	884±15
Resolute Bay	29-30/7/88	Bott.trawl [b]	48	147.8±3.9	48	28.3±2.2	802±15
Resolute Bay	12-31/8/88	Bott.trawl [b]	29	156.7±4.5	29	34.0±3.1	840±14
Resolute Bay	1-4/9/88	Trap net	40	177.7±3.7	38	40.8±2.1	746±10
Resolute Bay	29-30/7/89	Trap net	87	185.6±3.1	87	48.5±2.5	708±9
Resolute Bay	4-9/9/89	Trap net	37	173.2±4.9	37	37.7±2.8	687±17
Group mean (± SE)			6	163.5±7.3	6	36.2±3.2	778±32
NON-SCHOOL JUV.							
Resolute Bay	29-30/7/89	Trap net	45	89.0±1.5	45	5.0±0.3	674±11
Resolute Bay	9-11/8/89	Bott.trawl [b]	98	82.8±1.3	98	4.3±0.2	668±9
Resolute Bay	31/8-1/9/89	Bott.trawl [b]	116	86.8±1.2	116	4.9±0.2	686±9
Group mean (± SE)			3	86.2±1.8	3	4.7±0.2	676±5

[a] Trawl towed off the bottom, in the water column

[b] Trawl towed on the bottom

Table 2-2. Mean (± SE) stomach fullness (SF, scale 1-5), percentage of empty stomachs, and mean weight (± SE) of stomach contents (as % body weight) of samples from adult and juvenile Arctic cod schools, and non-schooling cod, 1985-91. Group means (± SE) are calculated from the means of individual collections.

Location	Date (d/mo/yr)	n	SF (1-5)	Empty (%)	n	Stomach wt. (%)
ADULT SCHOOLS						
Resolute Bay	21/8/86	43	3.28±0.16	0.0	-	-
Allen Bay	2/9/89	101	1.00±0.00	100.0	101	0.00±0.00
Allen Bay	16/9/89	99	3.19±0.14	17.2	36	1.61±0.23
Allen Bay	8/8/90	100	1.00±0.00	100.0	100	0.00±0.00
Allen Bay	15/8/90	101	1.98±0.12	44.6	101	0.68±0.13
Allen Bay	28/8/90	100	1.01±0.01	99.0	100	0.00±0.00
Gascoyne Inlet	18/8/88	179	1.13±0.04	94.4	179	0.05±0.02
Erebus Bay	19/8/88	89	2.36±0.12	30.3	89	0.82±0.11
Radstock Bay	31/7/91	97	1.04±0.02	95.9	97	0.03±0.02
Group mean (± SE)		9	1.78±0.32	64.6±13.7	8	0.40±0.21
JUVENILE SCHOOLS						
Resolute Bay	14,20/7/89	37	3.84±0.18	0.0	37	2.30±0.27
Resolute Bay	31/7/91	40	3.70±0.17	2.5	40	3.20±0.26
Group mean (± SE)		2	3.77±0.07	1.3±1.3	2	2.75±0.45
NON-SCHOOL ADULTS						
Resolute Bay	29-30/7/88	48	3.46±0.21	8.3	48	2.40±0.31
Resolute Bay	12-30/8/88	29	3.30±0.30	10.3	29	2.00±0.38
Resolute Bay	1-4/9/88	40	3.98±0.18	5.0	38	3.40±0.45
Resolute Bay	29-30/7/89	87	3.84±0.11	1.1	87	3.69±0.28
Resolute Bay	4-9/9/89	37	4.08±0.21	2.7	36	3.25±0.43
Group mean (± SE)		5	3.73±0.15	5.5±1.7	5	2.95±0.32
NON-SCHOOL JUV.						
Resolute Bay	29-30/7/89	45	3.22±0.18	4.4	45	1.86±0.26
Resolute Bay	9-11/8/89	98	2.64±0.11	11.2	98	1.29±0.13
Resolute Bay	31/8-1/9/89	116	3.12±0.12	12.9	116	1.79±0.15
Group mean (± SE)		3	2.99±0.18	9.5±2.6	3	1.65±0.18

Table 2-3. Mean sex ratio (number of males/females) and mean (± SE) gonad weight (as % body weight) of male and female schooling and non-schooling Arctic cod, 1985-91. Group means are calculated from the means of individual collections.

Location	Date (d/mo/yr)	n	Sex ratio (M/F)	Male Gonad wt. (%)	Female Gonad wt. (%)
ADULT SCHOOLS					
Resolute Bay	21/8/86	93	0.55	5.33±0.38	2.86±0.05
Allen Bay	26-27/7/89	35	0.75	-	-
Allen Bay	2/9/89	100	0.92	-	-
Allen Bay	16/9/89	98	1.04	-	-
Allen Bay	8/8/90	100	0.82	2.98±0.22	2.07±0.09
Allen Bay	15/8/90	100	0.89	3.27±0.11	2.33±0.11
Allen Bay	28/8/90	100	0.69	5.60±0.35	2.91±0.10
Gascoyne Inlet	8/8/85	77	0.64	2.44±0.05	3.37±0.13
Gascoyne Inlet	23/8/85	80	0.82	4.05±0.20	3.29±0.09
Gascoyne Inlet	18/8/88	179	1.08	3.81±0.16	2.99±0.08
Erebus Bay	19/8/88	89	0.71	-	-
Radstock Bay	31/7/91	67	1.23	2.70±0.16	2.41±0.22
Group mean (± SE)		12	0.85	3.77±0.42	2.78±0.16
NON-SCHOOL ADULTS					
Resolute Bay	9,26/8/85	34	0.62	3.83±0.54	2.03±0.13
Resolute Bay	7,8/1988	77	0.93	4.26±0.35	2.38±0.11
Resolute Bay	1-4/9/88	38	0.73	-	-
Resolute Bay	29-30/7/89	89	1.02	-	-
Resolute Bay	4-9/9/89	37	1.47	-	-
Group mean (± SE)		5	0.95	4.05±0.22	2.21±0.18

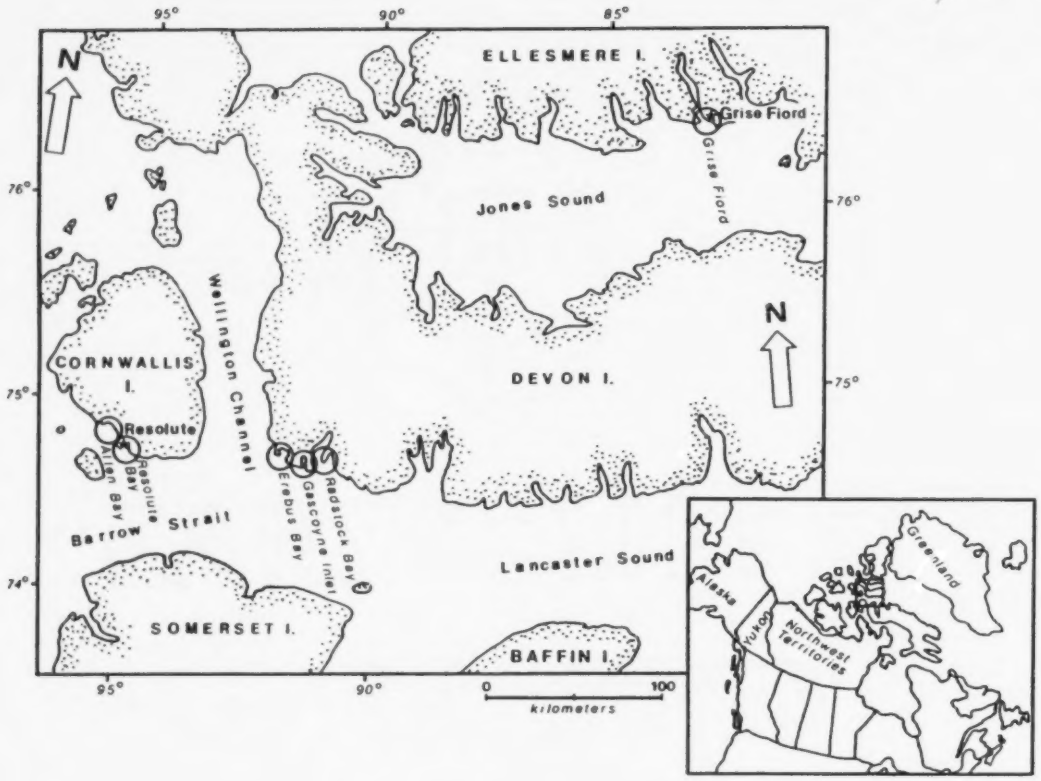

Figure 2-1. Sampling locations (circles) on the coasts of Cornwallis, Devon and Ellesmere Islands, N.W.T., arctic Canada, 1985-91. Stars indicate inhabited communities.

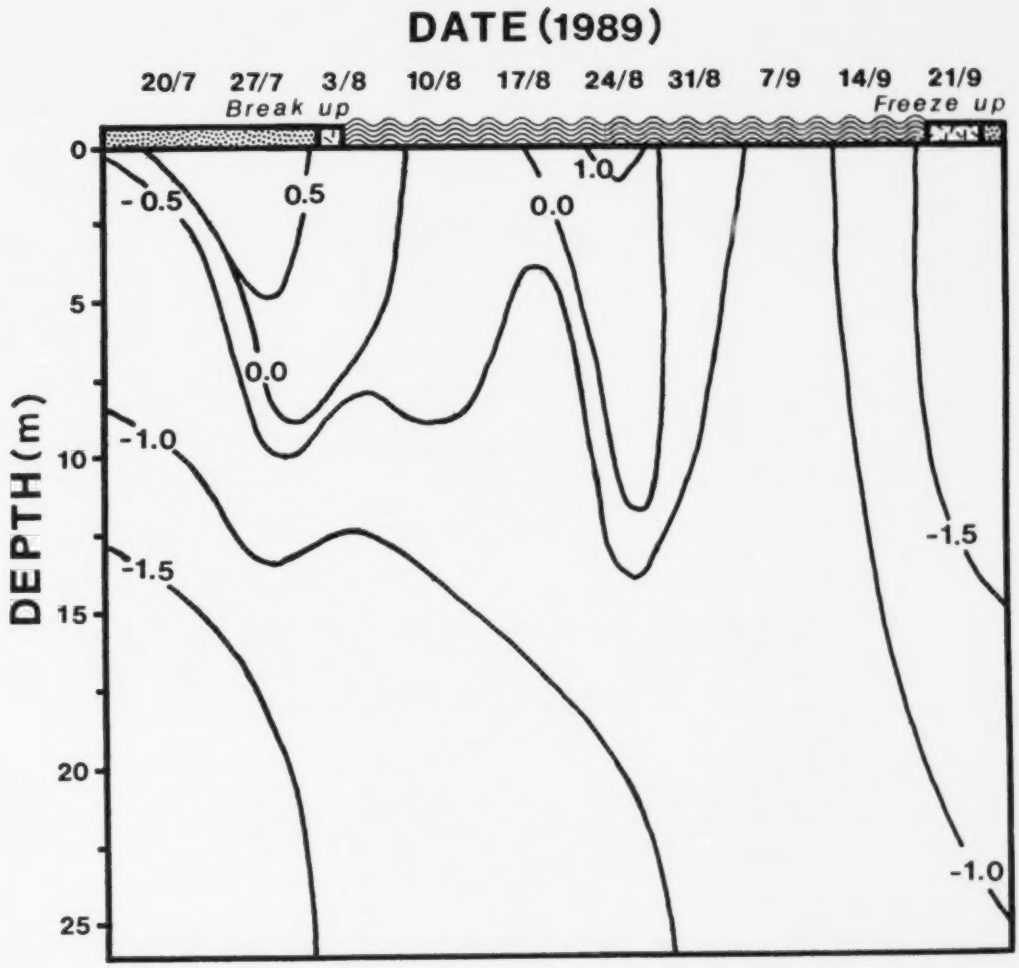

Figure 2-2. Isotherms for Resolute Bay, July-September 1989, drawn from weekly means of daily temperature records.

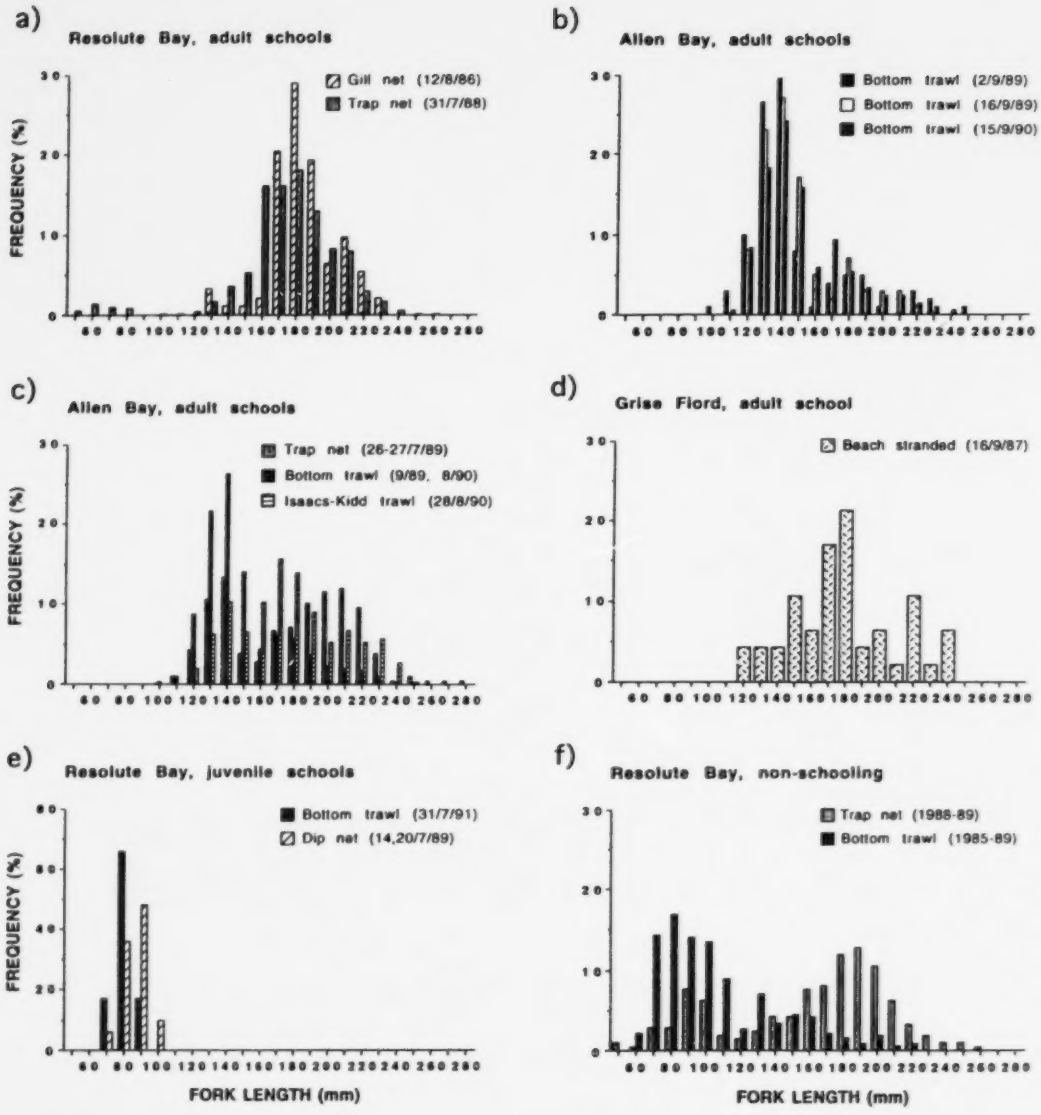

Figure 2-3. Fork length distributions of adult (a-d) and juvenile (e) schools, and non-schooling (f) Arctic cod.

a) Resolute Bay: gill net (n=93), and trap net (n=511).

b) Allen Bay: bottom trawl, 2/9/89 (n=101), 16/9/89 (n=99), and 15/9/90 (n=201).

c) Allen Bay: trap net (n=108), bottom trawl (n=401), and Isaacs-Kidd trawl (n=400).

d) Grise Fiord: beach stranded (n=47).

e) Resolute Bay: bottom trawl (n=100), and dip net (n=50).

f) Resolute Bay: trap net (n=210), and bottom trawl (n=326).

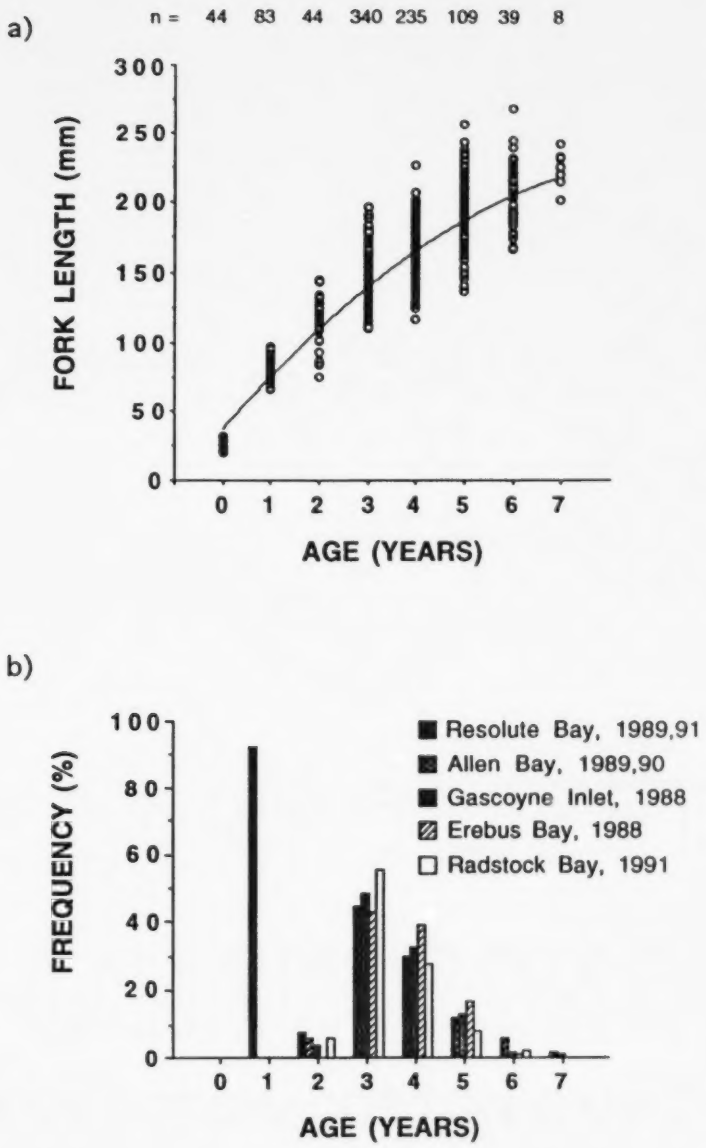

Figure 2-4. Age relationships for schooling Arctic cod.

a) Length-at-age. (age-0 individuals caught in plankton nets are added to include all year-classes). The curve is fitted by polynomial regression.

b) Age distributions of juvenile schools from Resolute Bay, 1989, 91 (n=90), and adult schools from: Allen Bay, 1989, 90 (n=438); Gascoyne Inlet, 1988 (n=108); Erebus Bay, 1988 (n=89); and Radstock Bay, 1991 (n=97).

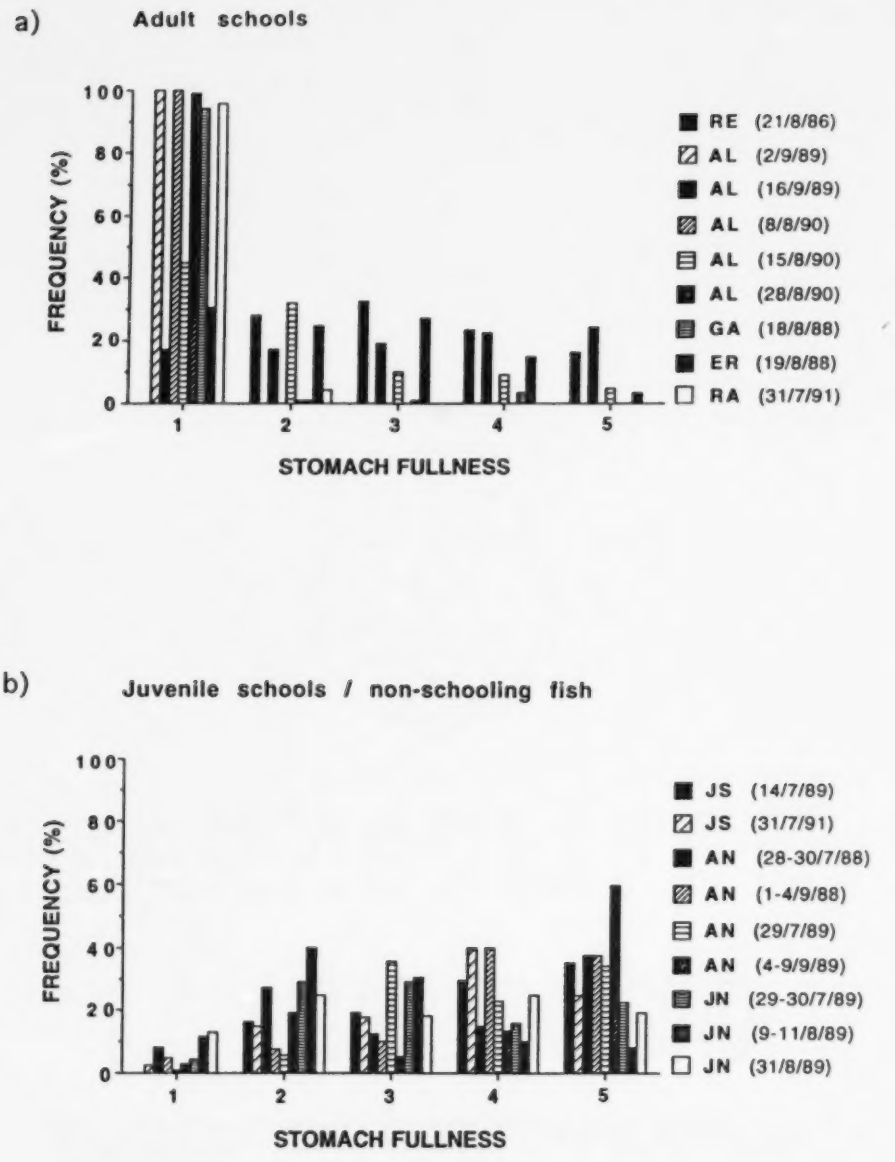

Figure 2-5. Distribution of stomach fullness for schooling and non-schooling of Arctic cod: (1) Empty, (2) < 1/3 full, (3) 1/3-2/3 full, (4) >2/3 full, (5) completely full and distended. a) Adult schools from: Resolute Bay (RE), Allen Bay (AL), Gascoyne Inlet (GA), Erebus Bay (ER), and Radstock Bay (RA).

b) Juvenile schools (JS), non-schooling adults (AN), and non-schooling juveniles (JN) from Resolute Bay.

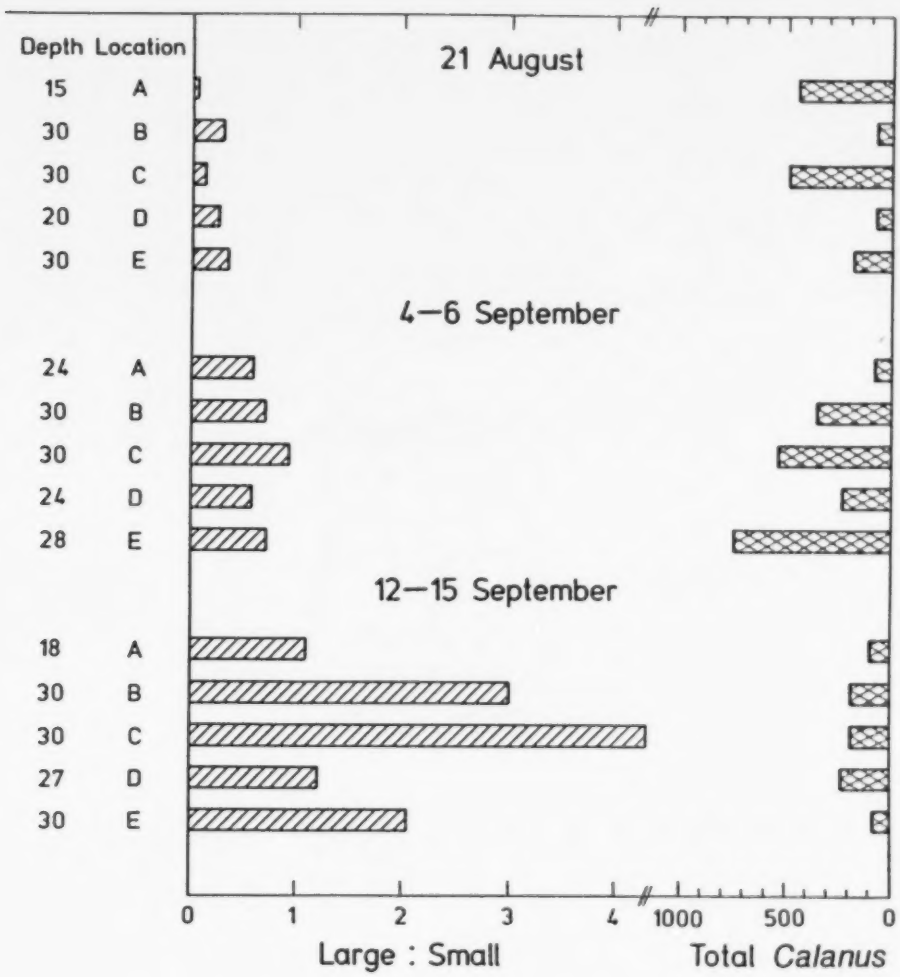

Figure 2-6. Calanoid copepods (Calanus hyperboreus and C. glacialis) captured in vertical plankton tows at different locations, 1990. On the left are ratios of large:small Calanus; the right half shows the total number of Calanus. Depth indicates the depth of the tow at each of the following locations:

A: a small basin between May Island and Cornwallis Island in Allen Bay, where Arctic cod schools were observed, 8 August - 4 September 1990 (Welch et al. 1993).

B: about 1 km south of location A, where there were no schools.

C: middle of Allen Bay, several km from Location A.

D: Resolute Bay.

E: Off-shore at a depth of 100 m, about 4 km outside Resolute Bay.

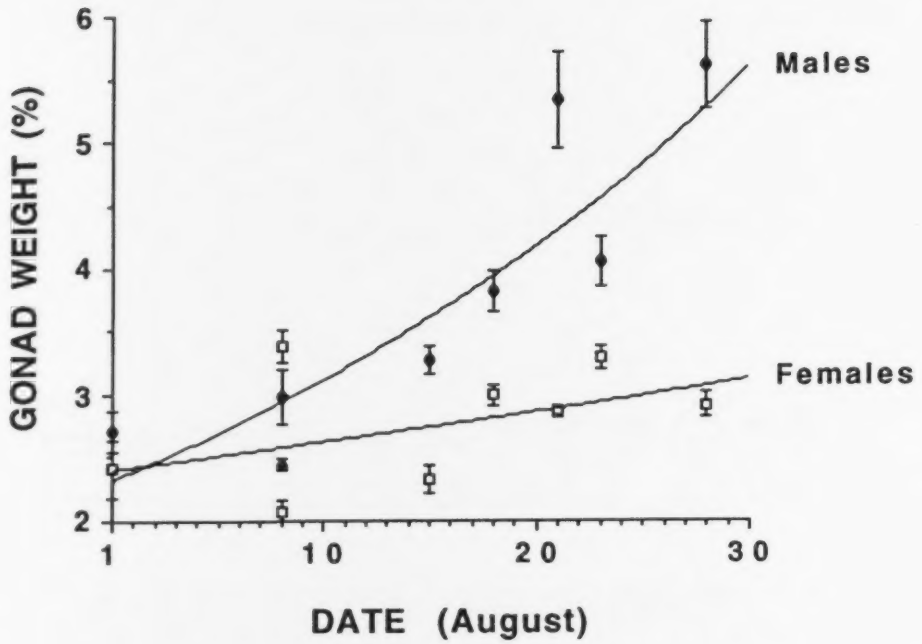

Figure 2-7. Mean gonad weight (± S.E.) as % body weight (=gonadosomatic index), for Arctic cod schools during August, 1985-91. Exponential curves are fitted to show gonad development over time (males, $r^2 = 0.796$; females, $r^2 = 0.214$).

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CHAPTER 3

Respiration of Arctic cod (Boreogadus saida): effects of acclimation, temperature, and food intake

A version of this chapter will be submitted for publication, as a manuscript co-authored with Mark S. Graham. Contribution no. 24 from the Resolute Marine Laboratory.

Introduction

Respiration rates in fishes are positively correlated with temperature, although rates for polar fishes may be elevated above those of more temperate fish at equivalently low temperatures (Brett and Groves 1979). Very few respiration studies have been done on any arctic fishes at ambient temperatures. Scholander et al. (1953) conducted some early investigations of respiration on Arctic cod (Boreogadus saida Lepechin, 1774) and fourhorn sculpin (Myoxocephalus quadricornis L.) at low temperatures, but only Holeton (1974) has thoroughly investigated respiration of arctic marine fishes at low temperatures. He also determined a relationship between body weight and respiration rate of Arctic cod at -1.5 °C. Arctic cod are subject to sub-zero temperatures during most of the year in the Canadian High Arctic (Hop et al., in press).

Most studies of respiration involving other gadids have been conducted at temperatures down to 3 °C, which is above the ambient temperature range of Arctic cod in this study. These studies have included Atlantic cod (Gadus morhua L.) (Saunders 1963; Edwards et al. 1972), Pacific cod (Gadus macrocephalus Tilesius, 1810) (Paul et al. 1988), saffron cod (Eleginus gracialis Tilesius, 1810) (Chen and Mishima 1986), and walleye pollock (Theragra chalcogramma Pallas, 1814) (Paul 1986). One study on Greenland cod (Gadus ogac Richardson, 1836) was conducted at temperatures down to 0 °C (Mikhail and Welch 1989). The majority of studies on respiration of polar fishes at < 3 °C have been conducted on antarctic fishes (e.g., Wohlschlag 1963, 1964; Ralph and Everson 1968; Morris and North 1984; Saint-Paul et al. 1988). These studies have generally found very low respiration rates at sub-zero temperatures.

The concept of metabolic cold adaptation implies that polar fishes would have elevated metabolic rates to enhance activity at low temperatures (Holeton 1974). Their metabolic rates would then appear higher than those expected

from extrapolating metabolic rates of temperate fishes to equivalently low temperatures (Krogh 1914; Scholander et al. 1953; Wohlschlag 1957, 1960, 1964). This phenomenon was reviewed by Holeton (1974), who dismissed it as a stress-induced artifact. He suggested that experiments showing elevated metabolic rates at low temperatures probably did so because they were conducted on excited fish with limited acclimation to laboratory conditions. However, Brett and Groves (1979) noted that Holeton's respiration values for Arctic cod were consistent with previously published (high) values for arctic fishes and did not dismiss the phenomenon of cold adaptation. In contrast, Clarke (1980, 1983, 1987, 1991) rejected completely the concept of metabolic cold adaptation, stating that it represents a cost to the organisms that has no selective advantage (Clarke 1991). If metabolic cold adaptation is related to acclimation time and handling stress, then a proper test would involve long-term acclimation of an arctic fish species before measurements of metabolic rates.

The first objective of this study was to compare metabolic rate of short-term and long-term acclimated Arctic cod to test Holeton's (1974) hypothesis regarding metabolic cold adaptation. Our prediction, consistent with Holeton's (1974) hypothesis, was that long-term acclimation would result in respiration rates predicted from extrapolating the relationship between metabolic rate and temperature, for temperate fish, to temperatures at which Arctic cod live. Other objectives of our study were to quantify the relationship between metabolic rate and temperature, within the range of ambient temperatures experienced by Arctic cod, and to measure specific dynamic action (SDA = increase in respiration or heat production after feeding) in both individuals and groups of Arctic cod.

Respiration values are essential for modeling energy budgets for this species (Hop et al., in prep.). We used the ambient temperature regime for high arctic waters and respiration values for starved and fed fish to model annual respiration budgets for Arctic cod. Respiration values for starved fish were

also used to model weight loss over time, and this was compared to actual weight losses of starvation groups.

Materials and Methods

Arctic cod were obtained from trap net catches in the Resolute Bay area, Cornwallis Island, N.W.T. (75°40' N, 95° W), during August-September, 1989 and 1990. They were transferred to the Resolute Marine Laboratory (Department of Fisheries and Oceans, Canada) in Resolute, and kept in a flow through system at ambient water temperature (0 °C ± 1.2 °C) and salinity (about 30 ‰).

Three respirometry experiments involving starved and fed fish were performed: 1) individual short-term acclimation; 2) individual long-term acclimation; 3) group trials.

The experiments included different sizes of fish, with mean weights of fish ranging from 6.2 to 20.2 g in the different experiments. Oxygen consumption was measured at constant (0.4 or 2.7 °C) and ambient temperatures (-0.5 °C to 1.2 °C). To allow direct comparisons among different experiments, VO_2 values were adjusted based on relationships of VO_2 with body weight and temperature. Fish weight was standardized to 10 g using Holeton's (1974) values for Arctic cod:

$\log (\text{Oxygen consumption } (\text{mg } O_2 \cdot h^{-1})) = 0.8301 \cdot \log W - 1.0485$

where W is wet weight (g). VO_2 values measured in short-term experiments at ambient temperatures were standardized to 0.4 °C (i.e., the lowest temperature used in the long-term experiment) based on the relationship between VO_2 and temperature we developed for short-term acclimated fish (see Results). Resulting VO_2 values were reported as $\text{mg } O_2 \cdot kg^{-1} \cdot h^{-1}$.

Individual short-term acclimation

Fish acclimated to aquaria in Resolute for a minimum of two weeks prior to experiments, were starved for at least one week to ensure post absorptive

condition. We used closed-system 455 ml Plexiglass respirometers placed in a dark flow-through water bath. Small magnetic spinbars in each respirometer prevented local oxygen depletion near the oxygen probe membranes. Individuals were acclimated to respirometers for a minimum of 24 h prior to measurements.

Oxygen concentrations were measured by calibrated Clarke-type oxygen electrodes (YSI-5739) with high-sensitivity membranes. Electrodes did not consume significant amounts of oxygen in the respirometers during 8 h blank runs. During experiments, recordings were done every 10-30 min after an initial equilibration period of about 1 h. Normally little or no spontaneous fish activity occurred after the equilibration period, and experiments were re-run if spontaneous activity was considered high or the magnetic stirrer malfunctioned. Oxygen consumption rates were determined from regressions of oxygen concentrations against time, coefficient of determination being > 0.90. Rates appeared to be independent of oxygen concentration until a critical low value at about 2 $mg \cdot L^{-1}$. The resulting routine values, reported as weight-specific oxygen consumption rates (VO_2), should be close to standard metabolic rates for short-term acclimated organisms at rest, although some spontaneous activity was included.

Individual long-term acclimation

Long-term acclimation was accomplished by shipping Arctic cod to the Vancouver Aquarium and keeping them for five months in a 1000 L recirculating-water aquarium at 0.4 °C and 29 °/oo salinity. Fish became conditioned to feeding and daily disturbances during this period. Respiration chambers and procedures were the same as in short-term experiments. After oxygen consumption measurements at 0.4 °C, temperature was gradually raised to 2.7 °C over two days, and fish were acclimated for at least 12 days to the new temperature.

Group trials

A group experiment on short-term acclimated Arctic cod (n= 349, mean wt. ± SE = 20.2 ± 0.3 g) was performed in an insulated round fiberglass tank (838 L) that contained a large magnetic stirrer. The water surface was sealed off from contact with air with black polyethylene, and the oxygen probe suspended in mid water.

Specific dynamic action (SDA)

SDA was determined as the difference between VO_2 values for fed and starved fish, and expressed as percentage of starved values. Significant differences ($p < 0.05$) were identified using t-tests (Zar 1974). Fish from the three previous experiments were fed the day before as well as the day of a trial to ensure that fish would be satiated so that measurements would reflect maximum elevations in respiration values (Jobling 1981). Fish were fed live copepods (Calanus spp.) in short-term experiments and frozen krill (Euphausia pacifica) in long-term experiments. The short-term fish first had to be conditioned to feeding in the lab. Live copepods are a natural food source, so fish started to feed within a few days when fed in groups, although it took longer (up to two weeks) to get individuals to feed in isolated chambers. Long-term acclimated fish had previously been accustomed to feeding on krill and fed individually to satiation within 30 minutes. Each fish was conditioned to the respiration chamber for one day, then transferred to a clean respirometer after feeding. In the group experiment fish were fed live copepods to satiation in the large respirometer over three days, and excess food was removed prior to measurements. Recording procedures were the same as in the previous experiments, with measurements starting 1 h after the last feeding. Corrections were made for increased water displacement after feeding, although unfed weights were used in the calculations of VO_2.

Acute temperature effects and maximum thermal range

Since the respiration experiments were conducted within a narrow range of ambient temperatures, and other studies (e.g., Craig et al. 1982) suggest that Arctic cod tolerate higher temperatures, we determined the survival of Arctic cod subject to a large temperature range. In this acute effect experiment, fish (n= 18, mean wt. ± SE = 20.3 ± 1.8 g) experienced a mean temperature increase of 0.7 °C · d^{-1} over a 28-day period. Fish were fed live copepods (Calanus spp.) daily, and thermal ranges of continued feeding and survival were determined.

Annual respiration budgets

An annual energy budget for Arctic cod was modelled based on an annual temperature budget for Resolute Bay and VO_2 values for starved and fed fish in the group experiment, using different durations of feeding centered around the period of peak temperatures each year. Arctic cod are known to feed during the summer/fall unless they appear in large schools (Hop et al., in press), and feeding during the winter has been recorded in Alaskan waters (Craig et al. 1982), although it is possible that fish in the Canadian High Arctic experience periods of starvation since otolith growth patterns indicate reduced growth rates during the winter (Bradstreet et al. 1986).

An annual temperature budget for Resolute Bay was developed with cumulative days indicated for each 0.5 °C interval. Ambient temperatures were measured at 5-6 m depth in Resolute Bay from July-September, 1988-90, and we supplemented these data with data (1984-86) from Bergmann (1989) to extend the record forward through April. The inter-year variation in temperatures during time of ice-cover is very low (Begmann 1989).

Respiration energy budgets (R = F + S), with energy units in kJ, included the following terms for various durations of feeding (F) and starvation (S):

$$F = \{ \sum_{i=1}^{5} [VO_{2\,(Ti)} + SDA] \cdot t_{(Ti)} \cdot f \cdot Q_{ox} \cdot 1.4788 \cdot 10^{-6} \cdot W^{0.8301} \} \text{ (kJ)}$$

$$S = \{ \sum_{i=1}^{5} [VO_{2\,(Ti)}] \cdot t_{(Ti)} \cdot (1-f) \cdot Q_{ox} \cdot 1.4788 \cdot 10^{-6} \cdot W^{0.8301} \} \text{ (kJ)}$$

where VO_2 is weight specific oxygen consumption and SDA specific dynamic action (mg $O_2 \cdot kg^{-1} \cdot h^{-1}$), T_i is mean temperature (°C), t is time (h) at each temperature, f is fraction of time spent feeding, Q_{ox} is oxycalorific coefficient, and W is wet weight (g). We used 30 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ as an approximate value for SDA. Mean temperature ranged from -1.75 to 0.25 °C, with each 0.5 °C temperature interval expressed as $T_i = (0.5\ i - 2.25)$ °C (Figure 3-2 b). Oxycalorific coefficients $Q_{ox} = 13.72 \cdot p + 13.36 \cdot (1-p)$ in J · mg^{-1} O_2, where p/(1-p) is lipid/protein ratio of the substrate being respired by starved and fed fish (Brett and Groves 1979; Brafield 1985). Starved fish likely use energy stored in the large liver for respiration, where a lipid:protein ratio of 14.94 gave a coefficient of 13.70 J · mg^{-1} O_2 (Hop et al., in prep.). Arctic cod in Resolute Bay feed predominately on copepods and amphipods, and energy for feeding fish originates from the diet. A 50:50 diet by weight of copepods (Calanus spp.) and amphipods (Parathemisto spp.), with respective lipid:protein ratios 1.62 and 0.65 (Hop et al., in prep.), resulted in a Q_{ox} of 13.54 J · mg^{-1} O_2.

Weight loss during starvation

Arctic cod rarely feed while schooling, and schools can persist in an area for up to two months (Welch et al. 1993; Hop et al., in press.). The mean condition of schooling fish was slightly lower than that of non-schooling feeding fish (Hop et al., in press), but weight loss over time for starving Arctic cod is unknown. We used the respiration budget for starving fish (S) and caloric values of Arctic cod to determine potential weight loss over time for different sizes of Arctic cod. Weight loss due to excretion and activity was not accounted for, but would likely add relatively little to the respiration energy budget. Weight loss (estimated % body weight lost) over time was expressed as:

$G = f \cdot S \cdot W^{-1} \cdot C^{-1} \cdot 100$

where f = duration of starvation, as a proportion of the year, S = respiration budget for starved fish (kJ), W = wet weight (g), C is caloric content of Arctic cod (mean ± SE = 6.459 ± 0.023 kJ · g^{-1} wet weight) (Hop et al., in prep.).

Modelled values for daily weight loss at 0 °C were compared to actual weight losses of Arctic cod determined experimentally for three size-groups of Arctic cod (mean weights = 12.0, 41.7, 53.2 g) at this temperature. The smallest size-group was acclimated for about two weeks, and the two largest size-groups for about seven weeks prior to measurements. Respiration values resulting from short- and long-term acclimation were used to model potential upper and lower limits of weight loss over time.

Results

Effects of temperature and acclimation

Weight-specific oxygen consumption (VO_2) for starved individuals of Arctic cod varied with temperature and acclimation time (Table 3-1; Figure 3-1). The relationship between mean VO_2 and ambient temperature for short-term acclimated Resolute fish was described well by linear regression: VO_2 (mg $O_2 \cdot kg^{-1} \cdot h^{-1}$) = 15.303 · T(°C)+ 83.712, (r^2 = 0.904, p = 0.0492). This represented a Q_{10} of 7.3 over a temperature range of 2.3 °C (-1.5 to 0.8 °C).

The mean VO_2 for long-term acclimated fish at 0.4 °C (46.56 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$) was significantly lower than that of short-term acclimated fish adjusted to the same temperature (88.71 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$; $p < 0.001$, Table 3-1). The temperature response curve for short and long-term acclimated fish was: VO_2 (mg $O_2 \cdot kg^{-1} \cdot h^{-1}$) = 11.306 · T (°C) + 42.131. This represented a Q_{10} of 6.9 over an experimental temperature range of 2.3 °C (0.4 to 2.7 °C).

The VO_2 value for short-term acclimated fish in the group experiment was lower than for similarly acclimated individuals but higher than for long-

term acclimated individuals (Table 3-1), even though the large respirometer allowed for some activity. Swimming speed (means ± SE) of similarly sized individuals (n= 12, mean length = 143.4 mm), in a group situation in a large tank (700 L with a 10 x10 cm grid on the front glass) was 2.90 ± 0.14 cm · s^{-1}, or 0.20 ± 0.01 body lengths · s^{-1}.

Effects of food intake

The increase in oxygen consumption after feeding to satiation (SDA) varied between 20.0 and 41.8 mg O_2 · kg^{-1}· h^{-1}, or 31.8 to 61.2 % of VO_2 values for unfed fish (Table 3-1). In all experiments there was a significant increase in VO_2 from the starved situation ($p < 0.05$), although increases varied with fish size, temperature, time after feeding, and whether the experiment involved individual fish or a group. Small fish had a greater (60.8 %) SDA than large fish (36.8 %), although average food intake (± SE) at satiation level, measured as percentage weight increase after feeding, was lower for small fish (9.7 ± 0.7 %) than for larger fish (15.0 ± 1.9 %). A temperature increase from 0.4 to 2.7 °C did not affect the magnitude of absolute SDA for small fish acclimated to these temperatures (Table 3-1), although relative SDA was much higher at the lowest temperature (60.8 vs. 39.6 %). One day after feeding, SDA dropped from 38.72 to 28.20 mg O_2 · kg^{-1} · h^{-1} for short-term acclimated fish, although the change was not significant ($p = 0.394$). SDA in the group experiment was similar (41.82 mg O_2 · kg^{-1}· h^{-1}) to that of short-term acclimated individuals, but the percentage increase was higher (62.2 %; Table 3-1).

Acute temperature effects and maximum thermal range

In the thermal range experiment, when temperature was increased 0.7 °C · d^{-1}, Arctic cod fed actively up to 13.2 °C. Swimming and feeding activities increased with temperature up to the maximum temperature for feeding. Lethal temperatures, LT-50 and LT-100, occurred at 15.4 °C and 19.8 °C, respectively,

although fish were not maintained at high temperatures for an extensive period of time to test for long-term survival and incipient upper lethal temperature. Mortality of controls kept at ambient temperatures during this period was zero.

Annual respiration budgets and potential weight loss

During most of the year (9 months) the temperatures in Resolute Bay remained below -1.5 °C (Figure 3-2a), dropping to a winter minimum of - 1.8 °C. Mean weekly temperatures rose above -1.5 °C for two months and above 0.0 °C for one month (25 July - 28 August). Water temperature reached a maximum of 1.2 °C for a few days, but the mean weekly temperature never exceeded 1.0 °C in any year 1988-90. The total number of degree days in the annual temperature budget was negative (- 505 °C · d) due to long periods of sub-zero temperatures (Figure 3-2b).

Our calculated values of total energy used annually in respiration were related to fish size and duration of feeding (Figure 3-3). For a 33.5 g Arctic cod, the mean size of schooling individuals (Hop et al., in press), the energy used for respiration would be is about 300 kJ · year^{-1}, if the fish fed for the whole year, and 200 kJ · year^{-1} if the fish starved. Converted to daily rates, these become 0.8 and 0.5 kJ · d^{-1} for fed and starved fish, respectively. In cold environments, such as Resolute Bay, Arctic cod can starve for extended periods without losing much weight, although small fish would lose weight faster than larger fish (Figure 3-4). Thus, a 10 g fish would lose about 15 % of body weight per month, but a 33.5 g Arctic cod would lose only 8 % of body weight per month of starvation (more if swimming activity is high).

Absolute weight loss for Arctic cod under experimental conditions (about one month at 0 °C) is very low (Figure 3-5a). Daily relative weight loss amounted to 0.18-0.36 % per day, depending on fish size. These values fell within the range predicted by respiration models for short- and long-term acclimated Arctic cod (Figure 3-5b).

Discussion

We found that long-term acclimation significantly reduced VO_2 for Arctic cod, and that the temperature response curve was shifted downward but parallel with the curve for short-term acclimated fish. The effect of acclimation on VO_2 was also partly demonstrated by Holeton (1974), who noted that after capture and handling two or more days were required for oxygen-uptake rates of Arctic cod to stabilize. However, he did not acclimate the fish for a longer time, even though the relationship showed that VO_2 continued to drop slightly over time. Holeton's (1974) VO_2 values were higher than those found for bottom dwelling arctic fishes, and consistent with previously published values for arctic fishes (Scholander et al. 1953; Wohlschlag 1957), although he did not attribute elevated respiration values to metabolic cold adaptation.

The basis for Holeton's (1974) comment against the concept of metabolic cold adaptation in arctic fishes related to the handling stress and condition of experimental animals. Saunders (1963) found that handling may increase oxygen consumption by 70 % in the Atlantic cod. Therefore, to obtain the most basal values for oxygen uptake, fish must be well adjusted to captive conditions. Our short-term (two weeks) acclimation VO_2 values for Arctic cod were consistent with Holeton's values, and they were also similar to values for Greenland cod that had been kept in respiration chambers at 0 °C for 60 h prior to measurements (Mikhail and Welch 1989). However, we found that VO_2 was significantly lower after long-term acclimation (5 months). Presumably tissues are also affected by acclimation time, since in vitro metabolic studies on Arctic cod tissue samples indicated that this pelagic gadid had an elevated capacity, with respiration rates being higher than those of tissues from more temperate fishes (Peiss and Field 1950). Metabolic rates of tissues from long-term acclimated fish have not been measured to verify this.

Our VO_2 value for long-term acclimated Arctic cod, measured at 0.4 °C, was still higher than Holeton's (1974) values for bottom-dwelling cottids measured at -1.5 °C, but the values become similar if the cottid VO_2 is adjusted to 0.4 °C, using our relationship for temperature. Our VO_2 was substantially higher than Wohlschalg's (1963) value for an antarctic zoarcid with "unusually" low metabolism (27.6 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$), although Wohlschlag measured a VO_2 intermediate between our short- and long-term values for two immature zoarcids of 10 g. A respiration study involving acclimated (> one month) Pacific cod (Paul et al. 1988), also found comparatively low VO_2 (48.0 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$) if their value is adjusted for fish size and temperature to a 10 g fish at 0.4 °C. These VO_2 values for long-term acclimated arctic fishes are consistently lower than values reported earlier for polar stenothermal fish in support of metabolic cold adaptation (i.e., Scholander et al. 1957; Wohlschlag 1964). Even though our values for long-term acclimated fish remain slightly above what would be expected by extrapolating rates from temperate eurythermal fishes down to equivalently low temperatures (Brett and Groves 1979), they show that the concept of metabolic cold adaptation has little reality, as suggested, but not demonstrated by Holeton (1974).

Variability in VO_2 values tends to increase at extremely low temperatures (Wohlschlag 1963). The high variation in respiration rates in our experiments was likely due to variable stress levels and spontaneous activity that could not be controlled. Due to this variation, linear and exponential temperature response curves fitted the data equally well, thus we chose the simpler linear model. Linear response curves have been found for sub-arctic gadids and flounders held within the thermal regime they normally inhabit (Paul 1986; Paul et al. 1988; Paul et al. 1990). However, Paul et al. (1990) indicated that linear temperature responses for sub-arctic species may be an artifact of the limited thermal range normally associated with their high-latitude habitats.

The effect of temperatures on respiration of Arctic cod resulted in substantially higher Q_{10} values (Q_{10} = 7, for a 2.3 °C range) than what have been reported for other gadids at higher temperatures (Q_{10} = 2 to 3) (Saunders 1963; Mikhail 1985; Chen and Mishima 1986; Paul 1986). However, Q_{10} values generally increase as temperature decreases (Winberg 1956; Fry 1964), and may become even higher if calculations are based on narrower temperature intervals (< 10 °C). For instance, Paul et al. (1988) estimated the Q_{10} for Pacific cod to be 6.0 over a 6.5 °C interval (1.0 to 7.5 °C) where the temperature response curve was linear, but a Q_{10} of 2.5 for an 11 °C interval (1.0 to 12.0 °C). The former is similar to the high Q_{10} we observed for Arctic cod, indicating that the metabolic processes are strongly influenced by temperature when it is close to zero. However, since annual temperature fluctuations experienced by Arctic cod in arctic waters are minor, this may have little adaptive significance.

The VO_2 for fish in groups was lower than that of similarly acclimated individuals. Saunders (1963) also found that crowding reduced respiration rates, attributing this to more restricted movements as fish are added to a respirometer. In our group experiment, however, fish density was about 20 % and biomass 50 % of that in individual experiments. We therefore attribute the lower VO_2 to a social effect associated with the presence of conspecifics.

Swimming activity probably contributed little to the VO_2 of fish in groups since Arctic cod were slow swimmers both in the laboratory and when schooling in nature (H. Hop, pers. obs.). Soofani and Priede (1985) found for Atlantic cod that a swimming speed of 0.2 body lengths · s^{-1} caused a 5.7 % increase in VO_2 at 10 °C, and indicated that increases in VO_2 during swimming may be positively correlated with water temperature. Arctic cod, with a slender body and forked tail, should be more efficient at pelagic swimming than Atlantic cod, and swimming activity in the group experiment would therefore elevate VO_2 only slightly above standard rates.

For slow swimming fish, SDA after feeding to satiation may take up to 98 % of the metabolic scope (Soofani and Hawkins 1982), implying that there is little left for activity. Soofani and Hawkins (1982) suggested that metabolic scope for cod has evolved to accommodate peaks in oxygen demand following feeding rather than peaks during locomotor activity associated with acquisition of food. This probably also applies to Arctic cod, suggesting that our maximum SDA values may be close to the maximum scope for the species.

In our experiment SDA ranged from 32-62 % of standard VO_2, which is similar to the SDA generally found for Atlantic cod (40-60 %; Saunders 1963; Soofani and Hawkins 1982) and Pacific cod (34-48 %; Paul et al. 1988). Saunders (1963), however, found SDA to be quite variable sometimes reaching 90 %. Measures of SDA percentages may become inflated if the initial (starved) VO_2 values are low, e.g., we found that the same absolute increase in SDA in three experiments resulted in SDA values of 32, 40, and 61 %, depending on the initial VO_2.

Temperature had little effect on the absolute increase in SDA for Arctic cod, but SDA as a percentage of standard rates decreased with increasing temperature since standard rates increased. Jobling and Davies (1980) similarly reported a lack of temperature dependence on SDA for plaice (Pleuronectes platessa L.). Saunders (1963) found that SDA decreased slightly with fish size, which was supported by our results in the long-term acclimated experiment.

Maximum SDA generally occurs within 12 h after ingestion of meals (Jobling 1981), and it increases with meal size (Jobling 1981). To ensure that we obtained SDA at its maximum, we measured VO_2 after fish had been fed to satiation on two consecutive days. When measurements were repeated the second day after feeding, we found that SDA decreased by 12 %. Similarly, Paul et al. (1988) found that SDA for Pacific cod decreased by 16 % by the second day. Saunders (1963) determined that SDA for Atlantic cod (at 10 °C) reached

a maximum within 2-3 hour after feeding, and that rates then declined over the next seven days. The SDA effect is linked to the rate of passage of food through the gut (Beamish 1974), and a correlation between the temperature-dependent gastric evacuation rate and duration of SDA has been demonstrated (Edwards 1971; Jobling and Davies 1979, 1980). Stomach evacuation time for Arctic cod is nearly two weeks at temperatures close to 0 °C (Hop and Tonn, in prep.), suggesting a similar duration for SDA, with the decline in SDA being slowest towards the end. Due to slow stomach evacuation rates, SDA for Arctic cod in the wild will probably remain elevated throughout periods of feeding.

Few studies have determined maximum thermal ranges or lethal temperatures for arctic fishes. Fry (1964) indicated that the Alaska blackfish (Dallia pectoralis Bean, 1880) probably has an upper lethal temperature of 20 °C. Scholander et al. (1953) found an upper lethal temperature for Pacific tomcod (Microgadus proximus Girard, 1854) of 15-20 °C. Craig et al. (1982) found that Arctic cod were tolerant of a wide range in temperatures (0.5-13.5 °C) and salinities (1-29 °/oo). The upper temperature for actively feeding by Arctic cod from Resolute Bay, about 13 °C, concurs with maximum temperatures in which Arctic cod have been captured in Alaska (Craig et al. 1982), but is above its normal thermal range in the Canadian High Arctic; this may represent a maximum temperature tolerance for the species.

The optimal temperature for Arctic cod has not been determined, but the species generally occupies temperatures between -1.5 and 3.2 °C in North Atlantic waters, particularly those at the lower end of that range (Lear 1979; Falk-Petersen et al. 1986; Monstad and Gjøsæter 1987). Den Beste and McCart (1978) found ontogenetic differences in temperature use, with adults caught in coastal locations at temperatures 1-3 °C, whereas young-of-the-year were found over a wider temperature range (1-8 °C). Ambient temperatures in Resolute Bay apparently represent the lower end of the thermal range for Arctic cod and is likely sub-optimal for growth.

The costs of reduced growth rates at sub-optimal temperature conditions may be outweighed by the benefits of reduced competition and predation. In the Lancaster Sound area the Arctic cod is the only abundant pelagic species, and the presence of antifreeze components (glycoproteins) in its blood (Osuga and Feeney 1978) has made it possible for this fish to exploit epontic or ice-associated invertebrates (Andriyashev 1970; Lønne and Gulliksen 1989). Larger predatory fishes are conspicuously absent, although marine mammals fill the predatory niche, particularly during the open water season (Welch et al. 1992). During the nine months of ice-cover, ringed seal (Phoca hispida) is the only predator present, but 60 % of its diet consists of Arctic cod (Welch et al. 1992).

During periods of starvation or low food intake, a low respiration energy budget may be advantageous Arctic cod rarely feed during periods of schooling (Hop et al. in press), and slower growth during winter and early spring, as determined from otoliths patterns (Bradstreet et al. 1986), may indicate low food intake during this time of the year. During periods of food limitation, other gadids undergo a marked loss in body weight and condition (Chen 1983), but no such data exist for Arctic cod due to the difficulties in sampling during the winter months. Our experimental findings showed that Arctic cod lost about 0.2 to 0.4 % body weight per day at 0 °C depending on the weight of the fish. Experimental starvation of walleye pollock, until death occurred after 106 days, involved a change in condition factor from 0.745 to 0.435, constituting a weight loss of 45-50 % (Smith et al. 1986). Using their values in our weight loss model, a 10 g and a 100 g Arctic cod might survive for up to 5 and 7.5 months, respectively, although recovery may not be possible if fish lose more than 30-40 % of body mass. The annual respiration budget, coupled with growth information (Moskalenko 1964; Bradstreet et al. 1986), suggests that Arctic cod must be feeding during parts of the winter season. Craig et al. (1982) found that Arctic cod fed on mysids during the winter in Simpson Lagoon and Stefansson Sound, Alaska.

Slow growth rates of Arctic cod mainly result from low daily food intake (Hop et al., in prep.). Low respiration costs at ambient temperatures will result in high growth efficiency during periods of feeding and low weight loss during periods of starvation, although low metabolism may also be limiting for growth. In this study, we have shown that respiration rates for Arctic cod vary with the duration of acclimation, temperature and food intake. This type of information will be important in calculating energy budgets for this species (Hop et al., in prep.) and will contribute to energy flow models for arctic marine food chains (e.g., Welch et al. 1992).

Table 3-1. Mean (±SE) oxygen consumption rates (VO_2) of starved and fed Arctic cod, and specific dynamic action (SDA), after short- and long-term acclimation. Treatments in experiments with individual fish included fish size and time after feeding. In addition, VO_2 was measured for a group of fish (mean of two trials with 349 fish in a large respirometer). VO_2 was adjusted to a 10 g fish at 0.4 or 2.7 °C, based on its relationship with weight or temperature. SDA (%) was calculated based on the adjusted means as ([fed-starved]/starved) · 100.

Treatment	# fish	Type	Fish size	Mean wt. (g)	Temp. (°C)	Mean VO_2 ($mg \cdot kg^{-1} \cdot h^{-1}$)	Adjusted temp. (°C)	Mean adjusted VO_2 ($mg \cdot kg^{-1} \cdot h^{-1}$)	SDA ($mg \cdot kg^{-1} \cdot h^{-1}$)	SDA (%)
Starved										
long-term	12	individual	small	6.53±0.40	0.4	50.06	0.4	46.56±2.17	-	-
long-term	6	individual	large	14.35±0.67	0.4	51.03	0.4	54.26±5.72	-	-
long-term	12	individual	small	8.09±0.29	2.7	75.32	2.7	72.66±6.61	-	-
short-term	19	individual	small	7.31±0.61	0.1	88.78	0.4	88.71±7.63	-	-
short-term	349	group	large	20.20±0.31	1.2	67.79	0.4	67.23	-	-
Fed										
long-term	12	individual	small	6.53±0.40	0.4	80.51	0.4	74.89±3.08	28.33±3.77	60.8±8.1
long-term	6	individual	large	14.35±0.67	0.4	69.82	0.4	74.24±6.12	19.98±8.38	36.8±15.4
long-term	12	individual	small	8.09±0.29	2.7	105.15	2.7	101.43±8.80	28.77±11.01	39.6±15.2
short-term [a]	12	individual	small	6.22±0.77	-0.5	116.96	0.4	127.43±9.04	38.72±12.00	43.6±13.5
short-term [b]	12	individual	small	6.22±0.77	-0.4	109.46	0.4	116.91±7.21	28.20±11.20	31.8±12.6
short-term	349	group	large	20.20±0.31	0.7	101.72	0.4	109.05	41.82	62.2

[a] measured the day of feeding
[b] measured the day after feeding

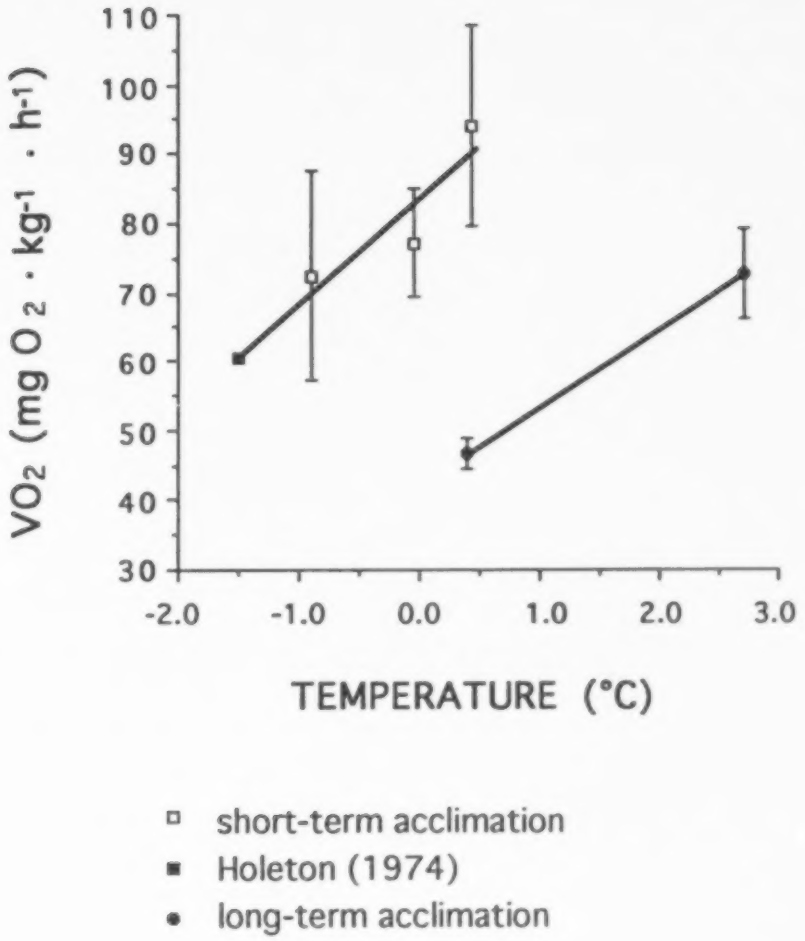

Figure 3-1. Weight-specific oxygen consumption VO_2 (adjusted to 10 g fish weight) of individual starved Arctic cod at ambient temperatures, following short (two weeks) or long (five months) periods acclimation. Values are means ± SE. Holeton's (1974) mean short-term (five days) value at -1.5 °C is included in the regression of VO_2 against temperature.

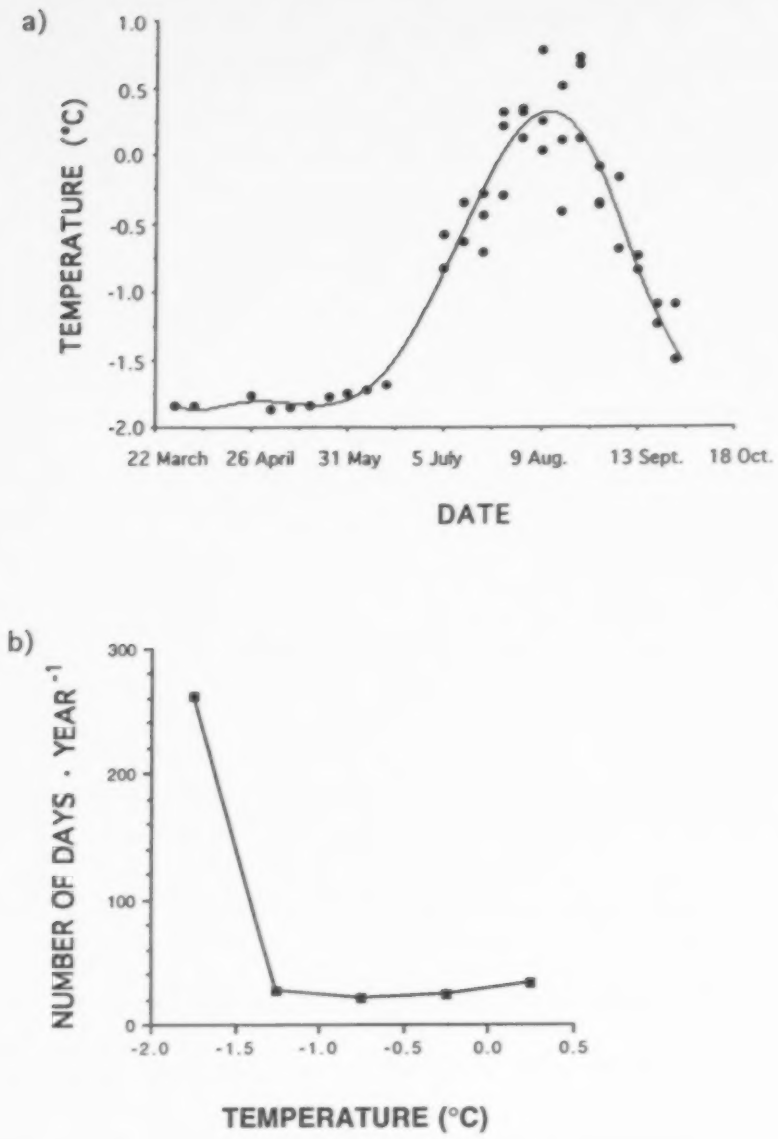

Figure 3-2. Water temperatures in Resolute Bay at 5-6 m. April-July data are weekly measurements, averaged over the period 1984-86, from CTD (conductivity, temperature, depth) profiles (Bergmann 1989). July-September data are weekly means based on daily measurements from water inflow to the Resolute Marine Lab., for each year 1988-90.

a) Temperature changes over time fitted by a polynomial regression.

b) Annual temperature budget, as cumulative number of days · year^{-1} indicated for each 0.5 °C interval.

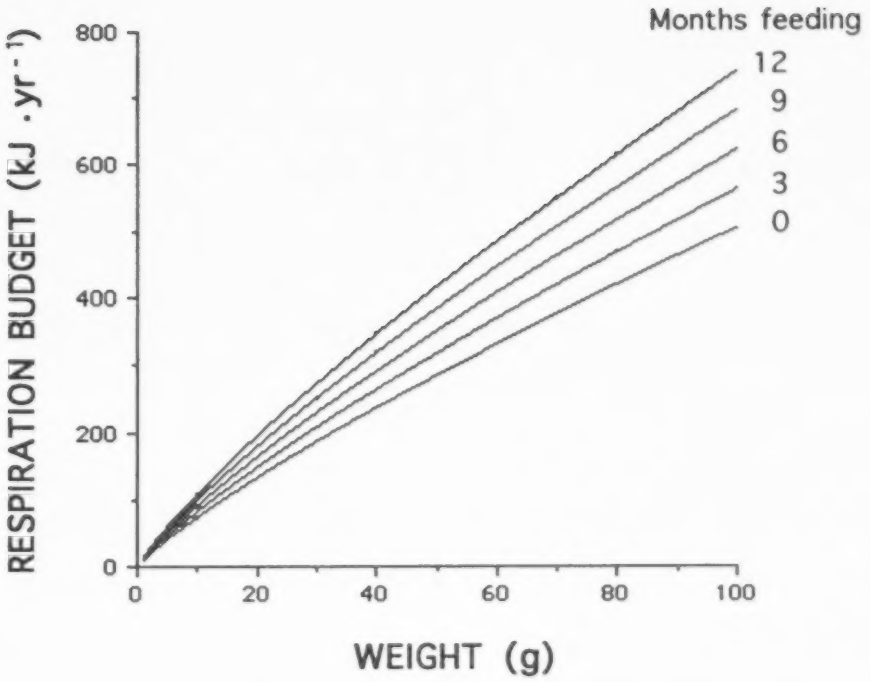

Figure 3-3. Annual respiration energy budgets for Arctic cod, based on different periods of feeding centered around the annual temperature maximum. Curves are modelled based on budgets of annual temperatures and VO_2 for a group of fed and starved short-term acclimated fish (n = 349).

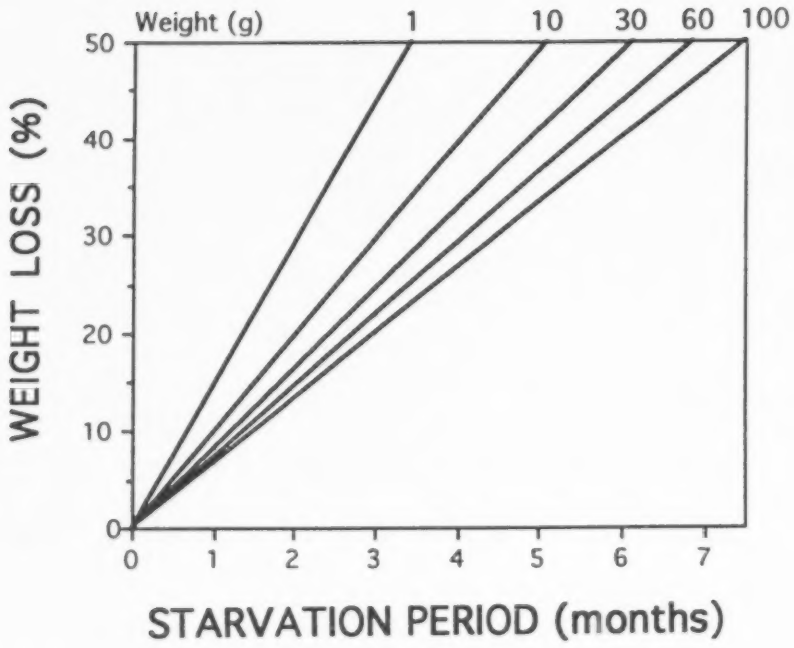

Figure 3-4. Estimated weight loss (% body weight) for starving Arctic cod in Resolute Bay. Curves are based on the energy contents and annual respiration energy budget modelled for starved fish of different sizes.

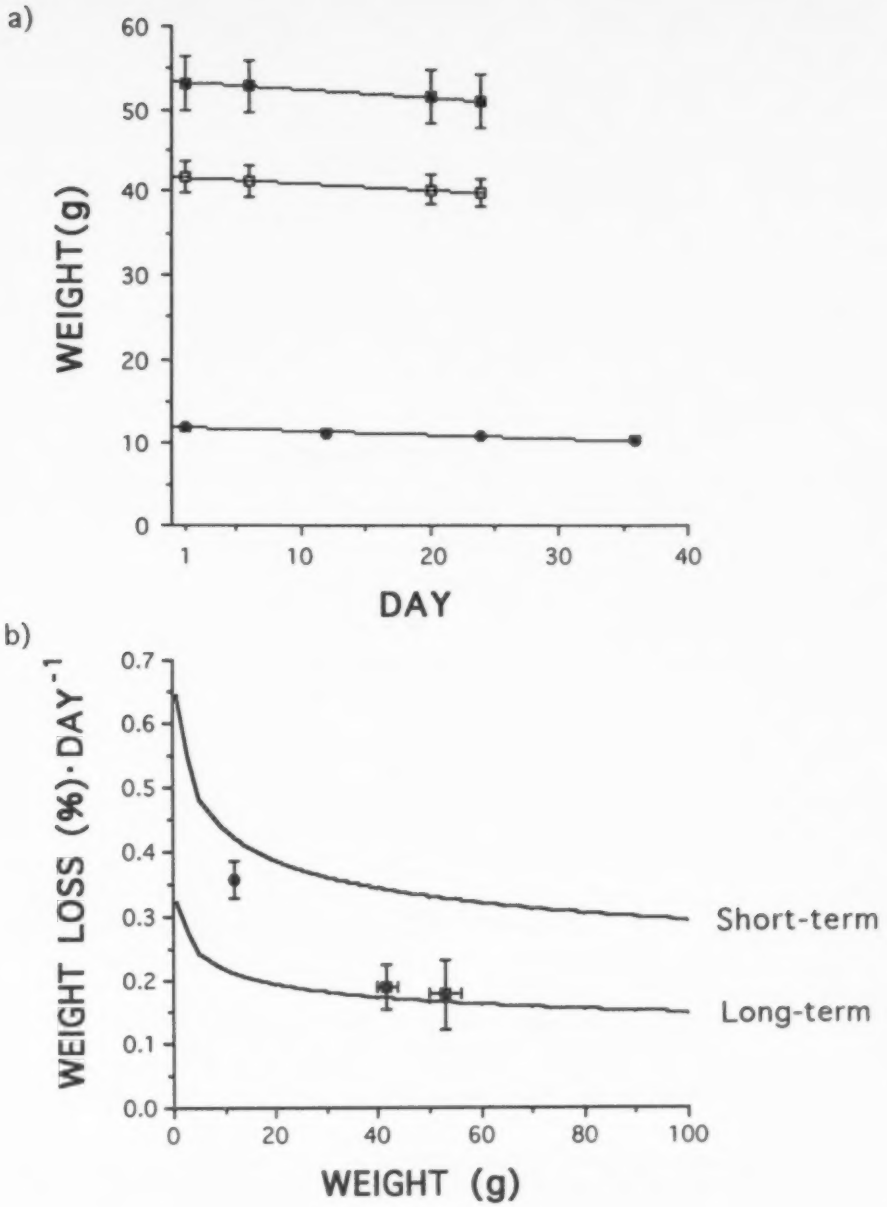

Figure 3-5. Weight loss for three size-groups of Arctic cod during starvation at 0 °C, with means ± SE indicated for each group. Acclimation time was two weeks for the smallest size-group and seven weeks for the two larger sizes.

a) Actual weight loss over time.

b) Daily weight loss (% body weight). Lines indicate weight losses predicted by respiration energy models for short- and long-term acclimated Arctic cod.

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CHAPTER 4

Spawning energetics of Arctic cod (Boreogadus saida) in relation to seasonal development of the ovary and plasma sex steroid levels

A version of this chapter will be submitted for publication, as a manuscript co-authored with Mark S. Graham and Vance L. Trudaeu. Contribution no. 26 from the Resolute Marine Laboratory.

Introduction

Spawning of Arctic cod (Boreogadus saida Lepechin, 1774) has never been directly observed in the Canadian Arctic, where this species is a key element in the marine food web (Hobson and Welch 1992; Welch et al. 1992). In general, little is known about the reproductive ecology and physiology of this species. The main reason is that Arctic cod typically spawn under the ice in the darkness of the arctic winter (Rass 1968). The only likely spawning area in arctic North America is in nearshore waters of the Beaufort Sea, in Steffanson Sound on the arctic coast of Alaska (Craig et al. 1982). One possible spawning site in the Canadian Arctic has been suggested by Bain and Sekerak (1978) to be at the north end of Wellington Channel in the vicinity of Sverdrup Channel, Queens Channel or Penny Strait, since larvae have been observed in early spring in the southern part of Wellington Channel in the southerly current between Cornwallis and Devon Islands. Larvae have also been caught in the westward counter current (Leblond 1980) on the south coast of Cornwallis Island during open water seasons (H. Hop, pers. obs.).

Most information on spawning of Arctic cod is from Russian waters (e.g., Nikol'skii 1954; Barenkova et al. 1966; Rass 1968), and to a lesser extent from the Alaskan Arctic (Craig et al. 1982) and northwest Atlantic (Lear 1979, 1980). Gonadal maturation starts in August (Bain and Sekerak 1978; Hop et al., in press), with male gonads starting rapid development sooner than females (Nikol'skii 1954; Hop et al., in press). At the time of early gonadal development, Arctic cod have been observed in large aggregations or schools in nearshore, shallow waters (Andriyashev 1954; Ponomarenko 1968; Bain and Sekerak 1978; Craig et al. 1982; Welch et al. 1993; Hop et al., in press). Spawning occurs from December to the end of March in the Barents Sea (Rass 1968), with peak spawning in January and February (Andriyashev 1954); it has been inferred that spawning occurs at a similar time in Alaskan waters (Craig et al. 1982). Maturation of females generally occurs at three years of age,

whereas males frequently reach maturity at two years (Lear 1979; Craig et al. 1982); in Russian waters maturity may be delayed until age-4 (Nikol'skii 1954). Female spawning output has been reported as 9,000 to 21,000 eggs, and Arctic cod eggs are the largest among gadid fishes (Andriyashev 1954; Matarese et al. 1989).

Laboratory studies of reproduction in Arctic cod have focused on artificial fertilization and embryonic and larval development of Arctic cod from Russian waters (Doroshev and Aronovich 1974; Aronovich et al. 1975; Altukhov 1981), especially effects of temperature, salinity and food consumption. Recently, we observed spawning of captive Arctic cod obtained from the Canadian High Arctic, and investigated incubation time, hatching, and growth and development of larvae (Graham and Hop, in prep.). The present study complements the latter study by investigating aspects of gonadal development, energy allocation and output. We also measured the plasma levels of sex steroids in Arctic cod as an endocrine correlation of gonadal function.

Materials and Methods

Arctic cod were caught in trap nets in Resolute and Allen Bays, Cornwallis Island, N.W.T., during late July-September, 1988-91. Fish were packed and transported (Graham and Hop, in prep.) from the Arctic to two laboratory facilities: Oceans Sciences Center (OSC), Memorial University of Newfoundland, St. John's (in 1988); and Vancouver Aquarium (VAQ) (in 1990, 1991). In the laboratories fish were kept in two 300 L tanks (OSC) or one 800 L tank (VAQ). Water temperatures were 0.2 ± 0.6 °C (OSC) and 1.0 ± 1.0 °C (VAQ), with respective salinities of 30.5 ± 1.5 °/∞ and 29.0 ± 1.0 °/∞. Fish were fed frozen capelin (Mallotus villosus Müller, 1777) at OSC and frozen krill (Euphausia pacifica and E. superba) at VAQ, 3-5 times per week.

Fish were sacrificed at different stages of gonadal development (July to February). Early samples (late July - September) included fish from Resolute

and Allen Bays, whereas later samples were fish from OCS (mid December) and VAQ (December - February). Fish were measured, weighed and sexed before livers and gonads were dissected out and weighed wet. Carcass weight was determined after removal of internal organs. For samples in December-February, carcass weight was estimated by subtraction of the weight of other organs (gonad, liver, otolith, intestines) from total weight; potential weight of stomach contents being included in carcass weight.

From these measurements, the following indices were calculated:
Gonadosomatic index (GSI) = (gonad weight/whole body weight) · 100,
hepatosomatic index (HSI) = (liver weight/fork length) · 100,
somatosomatic index (SSI) = (carcass weight/fork length) · 100.
The first index used gonad weight relative to whole body weight since this is the index most frequently reported in the literature (e.g., Crim and Glebe 1990; Smith et al. 1990; Kjesbu et al. 1991). The two latter indices used fork length (FL, mm) instead of whole body weight, since we were interested in absolute changes in these organs over time, not how they changed relative to the increasing total body weight during gonad development. These indices were standardized to the same fork length (245 mm, the mean length of ripe females, based on samples from July/August) to facilitate comparisons. The following linear regressions (with $p < 0.0003$ for all slopes) were applied in size corrections for females (F) and males (M):

F-HSI (%) = 0.029 · FL - 2.623, $r^2 = 0.550$

M-HSI (%) = 0.026 · FL - 2.417, $r^2 = 0.526$

F-SSI (%) = 0.183 · FL - 13.883, $r^2 = 0.902$

M-SSI (%) = 0.158 · FL - 10.845, $r^2 = 0.813$

Eggs were stripped at the time of spawning (mid February), determined as the time when fish first started to spawn in aquaria. Ripe fish could be easily stripped by applying pressure to the abdomen. Eggs remaining after stripping of ripe fish, and gonads of unripe fish, were removed by dissection. Potential fecundity (= mean number of eggs produced by ripe females) was determined

from 1.0 g sub-samples of gonads, and egg diameters of 22-25 fresh eggs were measured to the nearest 0.01 mm with calipers.

Gonad, liver and muscle tissues were dried at 60-70 °C to constant weight (3-5 days). Homogenized dried samples (1.0 g) were taken for ashing (595 °C) and caloric determinations (Adiabatic oxygen bomb calorimeter, model 1241) with results expressed in Joules (1 J = 0.2389 calorie). In addition, total protein was determined by the Kjeldahl nitrogen procedure (Bradstreet 1965), and total lipids were determined by chloroform/methanol extraction (Folch et al. 1957).

Relative composition of lipid classes was determined on an Iatroscan TH-10 TLC/FID analyzer using S-III Chromarods. This method involves separation of lipids on silica-coated rods and their subsequent detection by a flame ionization detector (Ackman 1981). Fresh gonadal and liver tissues were stored refrigerated in chloroform/methanol (2 : 1 by volume), and lipids were extracted by the Folch et al. (1957) method prior to spotting onto the chromarods. The rods were developed for 60 min in a solvent system of benzene/chloroform/acetic acid/methanol (49 : 8 : 0.3 : 0.2 by volume). Known standards of monoglycerides, diglycerides, triglycerides (glycerides = acylglycerols), phospholipids, cholesterol, cholesterol esters, and free fatty acids were run under identical conditions as the samples for peak identification. The standard for wax esters was lipid extracts from Calanus hyperboreus, which contains > 80 % of this lipid class during July-November (Lee 1974), although other non-polar lipids could also be present. Data were analyzed by Shimadzu EZ Chrom Data System.

Plasma levels of sex steroids were determined in ripe and unripe fish at the time of first spawning (mid February). Blood samples were taken from the caudal blood vessel, centrifuged for 20 min before the plasma layer was removed, conserved with merthiolate, and then immediately frozen. Concentrations of the sex steroid hormones estradiol [E_2], 11-ketotestosterone [11-KT], and testosterone [T] were determined by radioimmunoassay after ether

extraction (Van Der Kraak et al. 1984; Van Der Kraak et al. 1990; Wade and Van Der Kraak 1991). Since [T], by two different biosynthetic pathways, is a precursor for both [E2] and [11-KT] (Fostier et al. 1983), we determined the ratios of [E2] and [11-KT] to [T] to assess possible differences between ripe and unripe females.

Results

Gonadal development of Arctic cod started in August, with male gonads initially developing at a faster rate than female gonads (Figure 4-1a). Male gonads reached full size by early December, about two months prior to females. Gonads of ripening females developed exponentially (regression $p = 0.0001$; $r^2 = 0.981$). Arctic cod, held at VAQ, became ripe and started to spawn by mid February. The GSI of ripe female fish was high (mean = 47.7 %, range 38.5 - 52.5 %) (Table 4-1). However, at the time of spawning, 23 % of the females were still unripe, and had significantly lower GSI (20.2 %; t-test, $p = 0.0001$) than ripe females. Body weight with gonads removed, or length of unripe fish was not significantly different from those of ripe fish (t-tests, $p > 0.3$).

The hepatosomatic index (HSI) indicated that liver mass decreased close to spawning (Figure 4-1b), with most of the change occurring within the last two months. In ripe females, the HSI decreased from 5.4 % in July-September to 1.2 % in February, a drop of 78 %, whereas in unripe females the decrease was less (to 1.5 %). The single ripe male also had a much lower HSI at the time of spawning (0.7 %), as compared with unripe males in July-September (4.9 %) (Figure 4-1b).

The somatosomatic index (SSI), suggested that muscle mass changed little until just prior to spawning (Figure 4-1c). At spawning SSI declined by 5.0 % in ripe females (t-test, $p = 0.0006$) and by 6.7 % in the ripe male.

At the time of spawning, gonads of ripe females consisted of 92 % water, whereas gonads of unripe females had less water (76.5 %), since oocytes absorb

a substantial amount of fluid prior to being released (Table 4-1). Ripe female gonads contained 4.1 % protein and 1.2 % lipids based on wet weight (51.0 % and 15.2 % based on dry weight), as well as some ash (0.3 %) and other material (2.4 % in Table 4-1, but likely less than that since sample loss during analyses procedures was unknown), and their mean energy content was 1.84 kJ · g^{-1} wet weight, or 23.85 kJ · g^{-1} ash free dry weight. Gonads from unripe females had significantly higher (t-test, $p = 0.0001$) protein and lipid contents, 15.7 and 4.5 % of respective wet weights (66.8 and 19.3 % of respective dry weights), and thus higher energy content (25.58 kJ · g^{-1} ash free dry weight) than ripe females (Table 4-1).

During initial gonadal development, from August to December/January, female gonads increased significantly in both lipid and, especially, protein content (t-tests, $p < 0.05$; Table 4-2). Thus, the lipid:protein ratio of female gonads decreased from 0.38 in August to 0.27 in December/January as more protein was incorporated. This ratio then changed little prior to spawning, at which time it was 0.29 for both ripe and unripe females. A similar pattern was apparent in males, although the lipid:protein ratio was always lower than in females. The single ripe male had a lipid:protein ratio of 0.16 (Table 4-1).

Livers of females increased significantly in protein content ($p = 0.0002$), whereas for males it changed little (Table 4-2). In contrast lipid content in the liver decreased during gonad development, especially for females (t-test, $p = 0.0004$; Table 4-2). The relative amounts of specific lipid classes were different in gonads and livers (Table 4-2). Whereas livers contained mainly triglycerides (> 90 %), gonads contained little of this lipid class (< 7 %; Table 4-2). Gonads contained about 50 % phospholipids during early development, and the amounts increased to > 90 % closer to spawning. During the early stages of development gonads also contained a high proportion of wax esters (or possibly another non-polar lipid component). In addition, gonads and livers contained low levels (< 10 %) of cholesterol and free fatty acids. There were no major

differences in lipid class composition between males and females in either gonads or livers.

Potential fecundity was 26, 470 ± 1, 350 (SE) eggs for fish of 151 ± 7 g wet weight, which equaled 175 ± 9 eggs · g^{-1} wet weight for this size fish (Table 4-3). The mean egg diameter of stripped eggs, before water hardening, was 1.65 ± 0.03 (SE) mm. Ripe eggs were unpigmented, had a thin chorion and could easily be seen through the ovarian wall. There was no significant relationship between egg diameter of ripe eggs and gonad weight (r^2 = 0.043, p = 0.542) or potential fecundity (r^2 = 0.156, p = 0.229) (Table 4-3). Ripe gonad weight increased linearly with whole body weight (r^2 = 0.871, p = 0.0001), and fecundity increased with gonad weight or with whole body weight (Figure 4-2a). Fecundity (FE) also increased with fork length (FL), although this relationship was not significant (r^2 = 0.212, p = 0.154).

Energy invested in gonads was substantial for Arctic cod, although none of the Arctic cod that spawned naturally in the laboratory died, in spite of high energy loss during spawning. Total energy loss as spawning products (Table 4-4), increased with increasing gonad size and whole body weight (Figure 4-2b). The largest fish thus had the largest absolute energy loss since they had the highest reproductive output. In addition, energy was lost from liver and muscle (carcass) during the gonadal development period.

Energy losses from liver (EL) and carcass muscle (EC) were determined for females (F) and males (M) from indices (HSI, SSI) in July/August and February (Figure 4-1b, c) and the energy content of these tissues. Weight-specific energy content (mean ± SE) of liver and carcass in July/August ($time_1$), determined by bomb calorimetry, were:

EL_1 (F; M) = (21,956.8 ± 343.6; 24,066.5 ± 229.2) J · g^{-1}

EC_1 (F; M) = (4,419.0 ± 55.2; 4,230.9 ± 65.1) J · g^{-1}

Energy losses within liver and muscle tissues were not determined directly, although we estimated additional energy lost from livers based on their lipid and protein contents (Table 4-2) and energy values of lipids (36.2 kJ

$\cdot g^{-1}$) and protein (23.6 kJ $\cdot g^{-1}$) (Brett and Groves 1979; Jobling 1982; Brafield and Llewellyn 1982). Estimated mean energy content of livers in December/January ($time_2$) were:

EL_2 (F; M) = (11934.6; 21412.8) J $\cdot g^{-1}$

Energy content of liver was then assumed not to change within the last month prior to spawning, whereas energy content of muscle was assumed to be constant for the whole development period (i.e., $EC_2 = EC_1$).

Total energy loss from liver (TEL) and carcass (TEC) was then determined for each fish:

$TEL\ (kJ) = [(HSI_1 \cdot EL_1) - (HSI_2 \cdot EL_2)] \cdot FL \cdot 10^{-5}$

$TEC\ (kJ) = (SSI_1 - SSI_2) \cdot EC_1 \cdot FL \cdot 10^{-5}$,

where FL = fork length (mm); calculations were carried out separately for males and females.

Estimated energy loss during development and spawning was 430 kJ for ripe females and 370 kJ for the ripe male (Table 4-4). Potential energy loss for unripe females was 450 kJ, which was similar to ripe females. The similar total energy content of gonads from ripe (123 kJ) and unripe (116 kJ) females indicates that the difference in GSI between these groups mainly resulted from water uptake at the time of spawning. Even though ripe Arctic cod lost a substantial amount of body mass during spawning, direct loss as spawning products contributed < 30 % of the overall energy loss. Most (> 55 %) of the energy loss was from the livers, and < 20 % resulted from loss of muscle mass (Table 4-4). Ripe females lost 87.5 % and 16.0 % of the initial energy in liver and muscle respectively, whereas the ripe male lost 86.5 % and 23.0 % of the energy originally in these tissues. An unknown amount of energy was obtained from ingested food, since Arctic cod continued to eat during gonadal development until the time of spawning, but we assumed that most of this was lost as respiration and waste products.

Plasma levels of sex steroids [T], [E_2] and [11-KT], at the time of spawning, were significantly lower in ripe fish than in unripe fish (t-tests, p =

0.0001), although the ratio of [E2]/[T] was about 50 % higher in ripe versus unripe females (Table 4-5). In contrast, the ratio of [11-KT]/[T] was about 20 % higher in unripe females. The single ripe male had steroid levels similar to the ripe females, although the ratio of [E2] and [11-KT] to [T] was lower (Table 4-5).

Discussion

Arctic cod invest a large amount of energy in reproduction. Weight loss in spawning was 30-50 % higher than that of Atlantic cod (Gadus morhua L.), Pacific cod (Gadus macrocephalus Tilesius, 1810), and walleye pollock (Theragra chalcogramma Pallas, 1814) (Eliassen and Vahl 1982; Smith et al. 1988, 1990). Even though Arctic cod lost about 50 % of the body mass as eggs, this represented only 30 % of the estimated loss in energy during gonadal development and spawning. It was evident that Arctic cod used energy from the large liver, as well as from muscle mass, during gonadal development. We found that both mass and lipid content of the liver, and mass of muscle, decreased during gonadal growth. This is similar to what has been observed for spawning Atlantic cod, where females withdrew lipids from the liver and protein from somatic tissues (Dambergs 1964; Krivobok and Tokareva 1973; Kjesbu et al. 1991). Protein is assumed to be mobilized from the white muscle rather than the red muscle (Love 1960; Greer Walker 1971).

Our estimated energy loss from gonads may be slightly greater than actual loss during spawning, since some gonad mass may be retained after spawning; about 9 % for Pacific and Atlantic cod (Smith et al. 1990). However, Atlantic cod are batch spawners, releasing portions of eggs as they develop, whereas eggs of Arctic cod seem to mature at the same time, and females are thus capable of being complete or synchronous spawners (Graham and Hop, in prep.). Arctic cod probably retain little gonad mass after spawning, with

gonads regressing to a state indistinguishable from gonads of immature cod (Sameoto 1984).

Estimated energy loss from the liver was likely underestimated, since we had no estimate of the decrease in its energy content during the last month prior to spawning. There are no published estimates of energy loss in Arctic cod during gonadal development with which to compare our values. However, loss of initial energy from the liver was 71 % for Pacific cod (Smith et al. 1990), and 67 % for Atlantic cod (Eliassen and Vahl 1982). Our estimate of energy loss from livers in Arctic cod was about 15 % higher, but then Arctic cod lost about 50 % more body weight than the other gadids during spawning.

Energy loss from somatic tissue of Arctic cod may also have been underestimated, since we did not account for additional weight of stomach contents in samples near spawning. Stomach content of unripe Arctic cod of 245 mm fork length (mean size of ripe females) may comprise up to 17 % of body weight if fish are fed once to satiation (Hop and Tonn, in prep.), although long-term feeding to satiation may give substantially lower values (about 30 % of maximum, or 5 % of body weight) (Hop et al., in prep.). In ripe fish, gonads occupy most of the body cavity, so stomach capacity must be substantially reduced, and the weight of stomach contents in our experiment was probably < 5 % of body weight. We also did not account for loss in energy content of somatic tissue, but this loss is likely small compared to weight loss. Our estimate of energy loss from somatic tissue relative to liver (18 %) was still higher than for Atlantic cod (6 %), and our ranking of losses (liver, gonad, muscle, in descending order) was the same as for Atlantic cod (Eliassen and Vahl 1982).

Potential fecundity of Arctic cod in our study was higher than what is generally reported in the literature (e.g., Scott and Scott 1988) based on Russian studies (Andriashev 1954), although higher egg counts (30,000 - 67,000) have been recorded from Russian waters (Rass 1941). The lower fecundity in the literature could be explained by smaller spawning individuals.

Even though our relationship between length and fecundity was not significant, it did indicate an increase in fecundity with length, as has been shown for Greenland cod (Gadus ogac Richardson, 1836) and Atlantic cod (Morin et al. 1991). Furthermore, an exponential relationship between fork length and gonad weight has been shown for Arctic cod (Lear 1980), and we also found that fecundity increased with gonad weight. Andriyashev (1954) indicated that most Arctic cod in Russian waters mature at about 200 mm total length (FL = 192 mm) at age 4, which would imply a fecundity of about 15,000 eggs (from our relationship) or 11,500 eggs (estimate based on Lear [1980] and Figure 4-2a), which are within the range reported (9,000 - 21,000). Our largest fish had a fecundity up into the range reported by Rass (1941).

Egg diameter was similar to what was reported by Andriyashev (1954) from Russian waters (1.6-1.8 mm). There was no significant relationship between egg size and fecundity in our study. Arctic cod eggs are larger and fewer as compared to other gadids (Andriyashev 1954), and it is evident that they vary little in size among regions. Egg diameter has been found to increase during August and September (Craig et al. 1982), but the most rapid increase occurs just prior to ovulation when there is a massive influx of water into the oocytes (Kjesbu et al. 1992). It has been suggested that the mechanism is a breakdown of protein-phosphate into free amino acids, which gives rise to high osmolality and an influx of water (Craik and Harvey 1984). The unripe females might have had a delayed influx of water, and possibly could have spawned later time that season.

Eggs of polar marine invertebrates are usually large and rich in lipids, a phenomenon known as Thorson's rule (Thorson 1950). There is also a general negative correlation between egg size and development rate in marine invertebrates, and it has been suggested that the slow rates of development for eggs of arctic invertebrates are caused by large egg size rather than low temperatures (Clarke 1983). The same relationship should be valid for fishes, although it may be difficult to demonstrate since eggs of different species

generally experience different temperature regimes and light conditions during development. Hatching of Arctic cod eggs under laboratory conditions occurs after 26-60 days (Aronovich et al. 1975; Graham and Hop, in prep.), although it has been estimated to occur after 45-90 days in the Barents Sea (Rass 1948). Atlantic cod eggs (1.2-1.6 mm) hatch after 50-60 days at surface temperatures of -1.5 to 0 °C (Templeman 1981), which is similar to Arctic cod eggs at equivalent temperatures.

Even though the energy content of eggs from Arctic cod and Atlantic cod were similar (Hislop and Bell 1987), Arctic cod eggs contained less protein (51.0 %) and relatively more lipids (15.2 %) than Atlantic cod eggs (73-82 % protein and 6-16 % lipids; Lønning et al. 1988; Kjesbu et al. 1991). This suggests that the Arctic cod mobilizes less protein from muscle during gonadal development, likely because it has less muscle mass than the Atlantic cod. It is also possible that our protein values were low, since the total recovery of protein and lipids was lower than that of Atlantic cod. However, ripe Arctic cod eggs contain much more water (92 %) than eggs of Atlantic cod (72 %; Kjesbu et al. 1991), consistent with the latter containing more protein. In contrast to muscle, Arctic cod do have a large liver, from which lipids can be mobilized. A high amount of lipids in Arctic cod eggs may increase their buoyancy and possibly their freezing resistance.

Lipids in the gonads and liver of Arctic cod differed, with mainly phospholipids in gonads and triglycerides in the liver. Phospholipids in gonads likely result from the breakdown of triglycerides (triacylglycerols) in the liver. Both phospholipids and triglycerides share a common precursor (diacylglycerol), and synthesis from this precursor involves two different enzymes to yield the final compounds (Lehninger 1982). Little is known of polar fish lipids, apart from the utilization of triglycerides for buoyancy (DeVries and Eastman 1978; Eastman and DeVries 1982); triglycerides are also stored in Atlantic cod livers (Eliassen and Vahl 1982). In polar marine invertebrates the dominant storage lipid is always triglycerides, although

arctic copepods may also store wax esters and sterol esters at certain times of the year (Lee 1974; Clarke 1983). We detected only small amounts of wax esters in Arctic cod liver, although gonads contained relatively high amounts of wax esters and some cholesterol during early development. Ovarian lipids of many north-temperate fish are predominately phospholipids (Kaitaranta and Ackman 1981; Tocher and Sargent 1984). Both phospholipids and cholesterols are essential constituents of cell membranes (Geise 1966), and therefore important in gonadal development.

Sex steroid levels differed between ripe and unripe fish, with unripe fish having higher levels of each of the steroids investigated. The significance of lower steroid levels in ripe females is not known, but this is a common pattern that has also been observed in non-gadid species. For example, in both rainbow trout (Oncorhynchus mykiss Walbaum, 1792) (Scott et al. 1980) and Atlantic halibut (Hippoglossus hippoglossus L.) (Methven et al. 1992), sex steroid levels increased during gonadal development and declined around the time of ovulation. In our experiment, ripe fish were sampled at a time when fish began spawning and thus, sex steroid levels had apparently already declined in most ripe fish. The high steroid levels, combined with relatively high GSI, in unripe fish, suggest that these fish could have ovulated at a later time the same season. The general spawning time for wild Arctic cod may extend over several months (Rass 1968). More detailed studies are warranted to help clarify the endocrine changes associated with gonadal development and spawning in Arctic cod.

Although we did not study the significance of the differences in sex steroid levels between ripe and unripe females, it is known from other teleosts that increased sex steroid levels prior to the spawning period are important for the development of secondary sex characteristics (Fostier et al. 1983; Cardwell and Liley 1991), expression of sexual behaviors (Liley and Stacey 1983; Fostier et al. 1983), and hormonal control of ovulation (Peter 1983; Peter et al. 1991). The gonadal steroid estradiol-17β is the primary stimulator

of liver vitellogenin production (Ng and Idler 1983) and increased estradiol levels prior to spawning are essential for increased production of yolk and chorionic proteins (Oppen-Berntsen et al. 1990), which subsequently enhances the development of embryos.

Initially, male gonads developed more rapidly than female gonads, reaching full size about two months before females. Differential rates of gonadal development have also been noted in other studies of this species (Lear 1979), and this ensures that males are ready to spawn when females first start to ovulate. Ripe females likely cannot defer ovulation, and a slight timing mismatch in spawning readiness would lower the chance of successful fertilization.

Nikol'skii (1954) indicated that Arctic cod may spawn only once during their life cycle. The energy cost of spawning is high, and spawning mortality in nature may therefore be substantial. Moskalenko (1964) described post-spawning Arctic cod as completely emaciated, and noted cases where fish perished in large numbers after spawning. Mortality due to spawning may partly account for the low abundance of age classes > 4 years in samples of this species (Hop et al., in press). It has also been found that mature males are generally smaller than mature females (Craig et al. 1982; Hop et al., in press). This may indicate that males have a higher spawning mortality than females, since males start to spawn at an earlier age (age-2) (Lear 1979; Craig et al. 1982)

However, under laboratory conditions it has been observed that Arctic cod are repeat spawners that do not die after spawning (Graham and Hop, in prep.), and other factors may also enhance post-spawning survival. Arctic cod have low respiration energy costs (Hop and Graham, in prep.), and are able to resume feeding immediately after spawning (Graham and Hop, in prep.). Field samples from Russian waters did contain post-spawners, and indicated that fish fed both before (66.7 %) and after spawning (43.5 %) if food was available (Altukhov 1981). Arctic cod spawn under the ice at a time when most

predators, except ringed seal (Phoca hispida), are absent (Davis et al. 1980), which would reduce mortality of emaciated post-spawners due to predation.

Wild Arctic cod may therefore spawn more than once, in spite of high amounts of energy allocated to reproduction, but most wild fish probably spawn only two times during their relatively short life time. Repeated spawning for this species would likely enhance fitness, since the total reproductive output for an individual would be higher if the fish can spawn twice and spawn at a larger size when the fecundity is greater. However, the chance of an individual surviving to the next spawning season may be rather low because of high predation rates on this species during the open water season (Welch et al. 1992; Welch et al. 1993). A high energy investment in the first reproduction must be a successful strategy for Arctic cod, given the high abundance of this species in the Canadian High Arctic.

Table 4-1. Gonad composition (mean ± SE) of ripe and unripe Arctic cod, held for five months at the Vancouver Aquarium prior to spawning (14 February, 1992). GSI is gonadosomatic index, and percentage values relate to wet weight.

Maturity/sex	n	Length (mm)	Weight (g)	Gonad wt. (g)	GSI (%)	Water (%)	Protein (%)	Lipids (%)	Ash (%)	Other (%)	Energy ($J \cdot d^{-1}$)
Ripe females	17	245±2	141.2±5.8	67.5±3.2	47.7±0.9	92.0±0.2	4.1±0.2	1.2±0.1	0.3±0.0	2.4±0.0	1836.2±58.1
Unripe females	5	249±5	91.0±4.9	20.2±0.8	22.3±0.9	76.5±0.9	15.7±0.6	4.5±0.2	0.9±0.1	2.3±0.1	5781.8±235.0
Ripe male	1	233	77.4	23.0	29.7	86.3	9.8	1.6	1.7	0.6	2903.3

Table 4-2. Total protein and lipids, and relative composition of lipid classes, of gonads and livers of Arctic cod early (August) and late (December/January) in the gonadal development period. Lipid classes indicated are: triglycerides (TG); wax esters (WE); cholesterol (CH); phospholipids (PL); and free fatty acids (FFA). Blank values indicate levels below detection (with no distinct peaks). Data are means ± SE.

Organ/ lipid-class	August		December/January	
	Females (%)	Males (%)	Females (%)	Males (%)
GONAD:	(n=6)	(n=8)	(n=3)	(n=1)
Total protein	11.9±0.4	12.4±0.1	20.4±1.1	13.5
Total lipids	4.5±0.2	3.6±0.1	5.5±0.4	2.7
TG	2.9±0.3	6.5±2.8	4.4±0.9	5.1
WE	37.5±1.4	30.6±4.6	-	-
CH	2.7±0.4	5.8±0.7	1.6±0.4	3.7
PL	51.7±1.3	48.8±3.0	94.0±1.1	91.2
FFA	5.4±0.4	8.2±1.6	-	-
LIVER:	(n=9)	(n=7)	(n=3)	(n=1)
Total protein	5.6±0.5	4.6±0.3	11.6±1.3	5.2
Total lipids	59.2±3.3	65.1±2.5	26.6±4.4	57.2
TG	96.6±1.3	96.0±0.6	89.3±2.4	98.8
WE	1.5±0.6	2.2±0.6	-	-
CH	-	-	0.9±1.1	0.1
PL	1.3±0.3	1.2±0.2	9.7±3.2	1.2
FFA	0.6±0.5	0.7±0.3	-	-

Table 4-3. Potential fecundity estimated based on 1.0 g subsamples, containing 372 ± 21 (SE) eggs, taken from the middle of each gonad. Mean egg diameter (± SE) was determined from measurements of 22-25 fresh eggs.

Fish no.	Weight (g)	Gonad wt. (g)	GSI (%)	Fecundity (no. of eggs)	Egg diameter (mm)
1	201.4	97.7	48.5	32101	1.65±0.04
2	141.6	66.9	47.2	24692	1.67±0.04
3	123.2	62.0	50.3	25234	1.66±0.02
4	149.4	77.5	51.9	27358	1.48±0.04
5	156.5	71.5	45.7	23205	1.56±0.03
6	164.5	78.9	48.0	32822	1.49±0.03
7	127.0	64.8	51.0	20913	1.80±0.02
8	117.8	60.0	50.9	21360	1.68±0.05
9	160.9	82.6	51.3	26914	1.77±0.03
10	151.1	72.0	47.7	33251	1.68±0.04
11	166.8	73.7	44.2	23289	1.70±0.02
Mean	150.9	73.4	48.8	26467	1.65
SE	7.2	3.2	0.8	1353.4	0.10

Table 4-4. Mean energy loss (± SE) during gonadal development and spawning in Arctic cod. Loss from gonads as spawning products (TEG) was determined from weight and energy content of gonads (Table 1). Losses from liver (TEL) and muscle (TEC) were determined from decreases in hepatosomatic and somatosomatic indices, and the energy content of liver and carcass.

Maturity/sex	n	TEG (kJ)	TEL (kJ)	TEC (kJ)	Total (kJ)	Gonad (%)	Liver (%)	Muscle (%)
Ripe females	17	123.87±7.98	252.09±2.08	54.48±0.45	430.44±8.55	28.4±1.3	58.9±1.1	12.7±0.2
Unripe females	5	116.43±4.09	248.14±5.14	85.52±1.77	450.10±10.07	25.9±0.5	55.1±0.4	19.0±0.1
Ripe male	1	66.78	238.41	65.65	370.84	18.0	64.3	17.7

Table 4-5. Plasma levels of sex steroids in Arctic cod at the time of spawning (14 February, 1992), with mean (± SE) concentrations listed for the following hormones: Estradiol [E_2], 11-ketotestosterone [11-KT], and testosterone [T]. Ratios (%) of [E_2] and [11-KT] to [T] are indicated. GSI is gonadosomatic index for fish sampled.

Maturity/sex	n	GSI (%)	[E2] ($pg \cdot ml^{-1}$)	[11-KT] ($pg \cdot ml^{-1}$)	[T] ($pg \cdot ml^{-1}$)	[E2]/[T] (%)	[11-KT]/[T] (%)
Ripe females	15	47.2±1.0	272±31	503±184	1210±278	32.6±3.8	30.3±5.1
Unripe females	5	22.3±0.9	831±192	2853±276	6092±784	15.6±4.7	50.6±9.7
Ripe male	1	29.7	193	235	1787	10.8	13.1

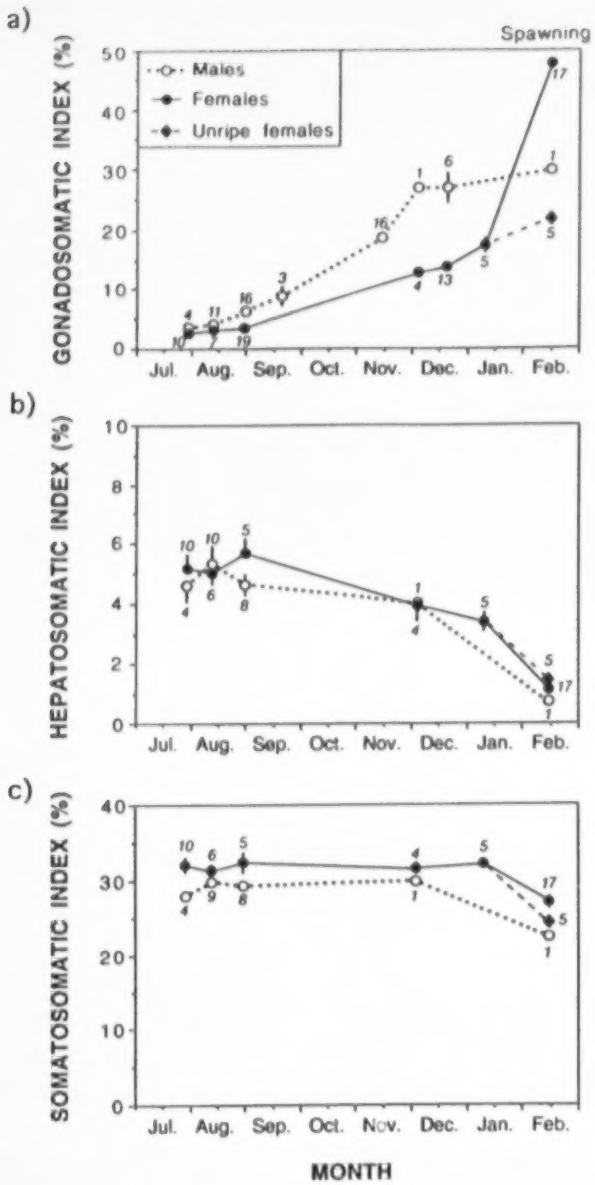

Figure 4-1. Gonadosomatic (a), hepatosomatic (b), and somatosomatic (c) indices for male and female Arctic cod during the season of gonadal development (numbers on graphs indicate number of fish). Unripe females were not in spawning condition when sampled at the time of spawning by ripe females (14 February). Data from July and August are from the Resolute Bay area (Hop et al., in press), data from mid September and November are from the Beaufort Sea, Alaska (Craig et al. 1982), and data from December - February are from Resolute Bay fish held at the Vancouver Aquarium and Ocean Sciences Center.

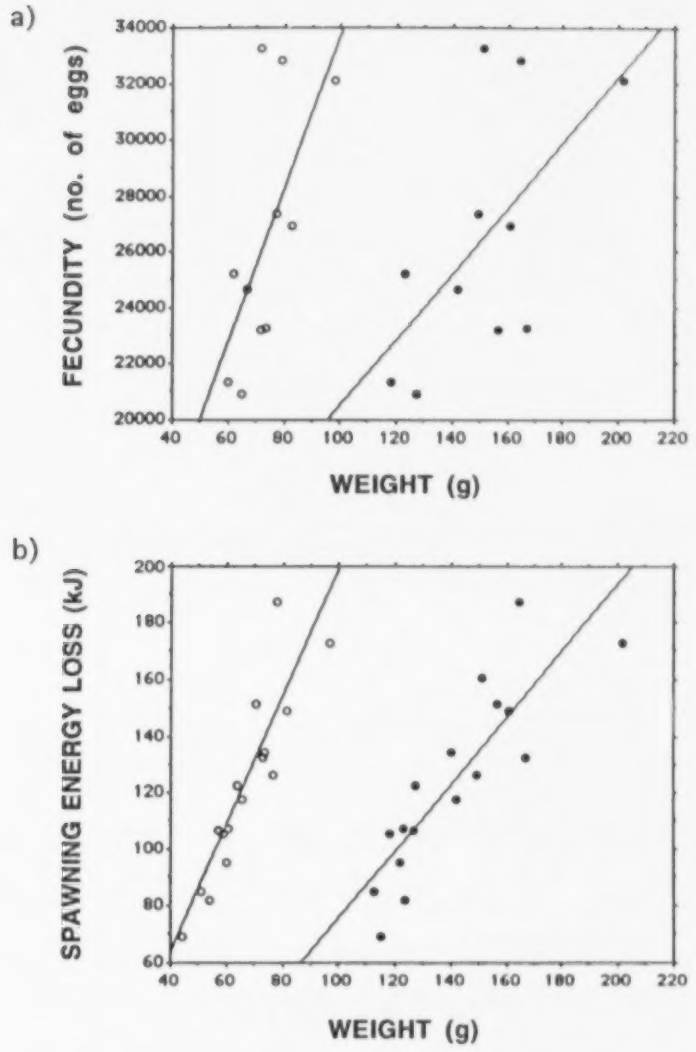

Figure 4-2. Potential fecundity (FE) and spawning energy loss (SE) of ripe Arctic cod, stripped at the time of spawning (February), regressed against wet weights of gonads (GW = open circles) and whole body (BW = filled circles).

a) Potential fecundity, as number of eggs:

$FE = 274.94 \cdot GW + 6{,}281.68$; $r^2 = 0.433$, $p = 0.0278$.

$FE = 116.81 \cdot BW + 8{,}837.12$; $r^2 = 0.382$, $p = 0.0427$.

b) Potential spawning energy loss, as energy contents of eggs:

$SE = 2.256 \cdot GW - 26.902$, $r^2 = 0.775$, $p = 0.0001$.

$SE = 1.181 \cdot BW - 42.887$, $r^2 = 0.733$, $p = 0.0001$.

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CHAPTER 5

Gastric evacuation rates and daily rations of Arctic cod (*Boreogadus saida*) at low temperatures

A version of this chapter will be submitted for publication, as a manuscript co-authored with William M. Tonn. Contribution no. 27 from the Resolute Marine Laboratory.

Introduction

Gastric evacuation rates have been used to estimate daily food consumption of several fish species (e.g., Windell 1966; Magnuson 1969; Elliott 1972; Elliott and Persson 1978; Persson 1979, 1982; Jobling 1981; Dwyer et al. 1987; Smith et al. 1989). During steady state conditions, the rate of gastric emptying will equal the rate of ingestion, so that daily ration can be estimated from evacuation rates for fish in their natural environment (Bajkov 1935; Tyler 1970). Gastric evacuation rates are positively correlated with temperature (e.g., Brett and Higgs 1970, Elliott 1972, Persson 1979, 1981), although for Atlantic cod (Gadus morhua L.) it was found that rates declined at temperatures above an optimum (Tyler 1970).

No studies have investigated gastric evacuation rates at very low temperatures. Most studies have been conducted at temperatures > 5 °C, although a few studies have extended the range down to 2-3 °C (Tyler 1970; Brett and Higgs 1970; Smith et al. 1989). It is unknown what happens to gastric evacuation rates at sub-zero temperatures, so extrapolation from experiments conducted at higher temperatures may not be appropriate. Polar marine fishes living at low ambient temperatures might experience very slow gastric evacuation rates, and such slow rates could limit daily food consumption and growth rates.

The Arctic cod (Boreogadus saida Lepechin 1774), a small arctic gadid, is subject to sub-zero ambient temperatures during most of the year in high arctic waters of Canada, and experiences little annual temperature fluctuation in the Resolute Bay area of N.W.T. (-1.8 to 1.0 °C; Hop et al., in press). We investigated gastric evacuation rates for this species at sub-zero ambient temperatures in experiments involving different natural foods (arctic zooplankton) and feeding regimes. Resulting gastric evacuation rates were applied in estimates of food consumption for Arctic cod in the field.

Materials and Methods

Arctic cod were obtained by trap nets from Resolute and Allan Bays, Cornwallis Island, N.W.T., Canada, in late July - early August, 1989-90. They were transferred to the Resolute Marine Laboratory (Department of Fisheries and Oceans Canada) and kept in a flow-through system, at ambient water temperature.

1989 experiments: effect of fish size and diets

Fish were acclimated to the laboratory for two months prior to experiments and fed natural zooplankton regularly during this time. Four experimental groups of 34-38 fish each were formed from the combinations of two size-classes and two diets; small fish (mean wt. = 6.6 g) and large fish (mean wt. = 45.0 g) were fed live copepods (Calanus spp.; mainly C. hyperboreus and Calanus glacialis) or amphipods (Parathemisto spp.; predominately P. libellula). These prey groups are also important food organisms for wild Arctic cod in the Resolute and Allen Bay area (Bain and Sekerak 1978; Hop et al., in press).

The fish were fed to satiation once at the onset of the experiment, conducted at -1.42 ± 0.07 °C (mean ± SE), and were then sacrificed over time to determine gastric evacuation rates. Stomach contents were weighed to nearest 0.001 g, after removing excess water.

Energy of dried (60-70 °C) prey and stomach contents were determined by adiabatic oxygen bomb calorimetry. The energy change of stomach contents, during digestion, was only measured in the 1990 experiments. Total protein content was determined by the Kjeldahl nitrogen procedure (Bradstreet 1965), and total lipid content by chloroform/methanol extraction (Folch et al. 1957).

In a separate experiment conducted at the same temperature, small fish (mean wt. 5.7 g, n=28) were fed one meal of P. libellula injected with chromic oxide (Cr_2O_3), before receiving undyed plankton in subsequent meals. Chromic

oxide is not assimilated (Windell et al. 1978), and passage time of food through the intestinal tract can be determined by the appearance of green faeces. This experiment included fish that had previously been on various diets, and they were not fed to satiation on dyed food.

1990 experiments: effect of single versus multiple meals

We investigated the effect on gastric evacuation rates of single versus multiple meals on two groups (each n=60) of medium-sized fish (mean wt. = 21.3 g) at -0.49 ± 0.08 °C (mean ± SE). Fish used in this experiment came from a large school that had not been feeding prior to capture (100 % empty stomachs). The fish were acclimated to the lab for about three weeks. During this time they were starved for two weeks and then fed live copepods (Calanus spp.) to satiation during the last 5-6 days prior to gastric evacuation experiments. The feeding history for these fish was thus different from that of the 1989 fish. During the experiment, one group was not subsequently fed, whereas the other group was fed live amphipods (Parathemisto spp.) daily. Evacuation rate of copepods was determined as in the 1989 experiment. For fish that were fed multiple meals, the orange copepod fraction was easily separated from the black amphipod fraction since the fractions mixed little in the stomachs.

Maximum stomach fullness and intestinal tract morphology

In a separate experiment, maximum weight of stomach contents of copepods Calanus spp. was determined for a size range of Arctic cod (13-68 g) fed to satiation before being sacrificed. We define stomach fullness as stomach content wet weight as a percentage of wet body weight (whole body - stomach content), maximum stomach fullness as the maximum wet weight of stomach content as a percentage of wet body weight (whole body - maximum stomach content) for fish fed to satiation on an empty stomach, and relative stomach fullness as stomach fullness as a percentage of maximum fullness.

Finally, we provided a detailed description of the intestinal tract morphology of Arctic cod since no such information exists in the literature. Identifiable sections of the intestines were measured and pyloric caeca counted.

Estimates of evacuation rate

Both exponential and linear regression functions of gastric evacuation were calculated, and the function with the highest coefficient of determination was used. The exponential function was of the form:

$$W_t = W_o e^{-Rt}$$

where W_t (stomach fullness) is the relative amount of food remaining in the stomach at time t (h), W_o is the intercept of the function (should be close to maximum stomach fullness when fish were fed to satiation at the onset of the experiment) and R is the instantaneous rate of evacuation (h^{-1}).

The linear function was of the form:

$$W_t = W_o - Rt$$

where W_t and W_o are as above, and R is the rate of evacuation for a linear decrease (h^{-1}).

Slopes (R) were compared using t-tests (Zar 1974). Exponential functions were semi-log transformed prior to testing to obtain linear relationships. Evacuation half-time was determined as the time when half of the content of a full stomach was evacuated. For an exponential function, this term has also been referred to as half-life, t_{50} (Booth 1990). Daily evacuation rates ($g \cdot d^{-1}$) were determined from the functions for the first day (24 h) and at half-time (± 12 h of the half-time point).

Field estimates of daily ration

Non-schooling Arctic cod were obtained from Resolute Bay, N.W.T., small fish by trawls, and large fish by a trap net that was emptied every 6 h, during three periods in July-September 1989. Diurnal variation in stomach fullness and relative stomach fullness was determined for each period. Daily rations were estimated from stomach fullness values and gastric evacuation rates determined from the experiments involving small and large Arctic cod fed Calanus spp. The Elliott and Persson (1978) model was used to estimate daily ration:

$$\sum C_t = (Rt)/(1-e^{-Rt}) \sum_{i=1}^{m} S_i (1-e^{-Rt}) = 24 \bar{S}R$$

where R is the instantaneous rate of gastric evacuation (h^{-1}), t is the duration (h) of each interval (i) over which stomachs were collected (= time of sampling ± 3 h), S is the mean stomach fullness, m is the total number of intervals in a 24-h day, and $\sum C_t$ is daily ration in terms of percentage of body weight. $\bar{S}$ (= $\sum S_i/m$) is the mean amount of food in the stomach over a 24-h period.

Results

Gastric evacuation patterns in 1989 were best fitted to exponential regression models (r^2 = 0.516 to 0.828) (Table 5-1; Figure 5-1 a-d). Curvilinear gastric evacuation curves imply that greater quantities of digested food move out of the stomach during the first hours than towards the end of digestion. Evacuation rates within the first 24 hours were similar for small fish fed different diets, with a mean value of 0.22 g · d^{-1} or 3.3 % body weight · d^{-1}. Large fish had higher absolute rates (0.78 g · d^{-1}) and lower relative rates (1.7 % · d^{-1}). Evacuation rates at half-time (± 12 h) were 0.14 g · d^{-1} for small fish and 0.45 g · d^{-1} for large fish, or 2.0 and 1.0 % body weight · d^{-1}, respectively (Table 5-1). Gastric evacuation half-times varied from 36 to 70

hours in the different experiments (mean = 51 hours). There was no significant difference in gastric evacuation rates between small and large fish fed Calanus spp. (t-test for slopes of semi-log transformed data, $p = 0.059$) or Parathemisto spp. ($p = 0.220$). In addition, there was no significant difference between evacuation rates resulting from different diets for small ($p = 0.076$) and large fish ($p = 0.198$). In the experiment with small fish fed chromic oxide injected amphipods, it took 48 h for 10 % and 108 h for 30 % of the fish to pass dyed food through the entire intestinal tract. The experiment was not continued past 120 h.

In the 1990 experiment gastric evacuation patterns were best fitted by linear regressions ($r^2 = 0.435$ to 0.508) (Table 5-1; Figure 5-1 e-f). The resulting evacuation rates, about 0.15 $g \cdot d^{-1}$ or 0.7 % body weight $\cdot d^{-1}$, were considerably lower than for both small and large fish in 1989. Stomach evacuation half-time averaged 153 hours in the two experiments, which implies that it takes 12-13 days for stomachs to empty. Continued feeding of the fish in the second experiments did not alter the stomach evacuation rate of the original meal significantly (t-test for slopes, $p = 0.374$).

Stomach wet weight, after feeding to satiation in experiments, varied between 6.3 % and 12.2 % of whole body weight (W_o in Table 5-1), with no clear size-related stomach weight pattern. When a larger size-range of fish were fed to satiation there was a weak ($r^2 = 0.356$) but significant ($p = 0.003$) positive relationship between fish weight (wt. range 13-68 g) and maximum stomach fullness (range 8-16 %). Maximum wet and dry weights of stomach contents varied significantly with fish weight in a log-log relationship ($r^2 = 0.828$) (Figure 5-2).

The prey used in the stomach evacuation experiments had different energy contents and protein/lipid ratios. Calanus spp. contained 29.360 ± 0.463 kJ $\cdot g^{-1}$ dry weight (mean ± SE) and 1.63 ± 0.06 lipid/protein, whereas Parathemisto spp. contained significantly less (t-test, $p = 0.0001$) energy (20.726 ± 1.094 kJ $\cdot g^{-1}$), mainly because they contained less lipid (0.63 ± 0.06 lipid/protein).

Calanus spp. also had significantly higher (p= 0.0001) dry/wet weight (%) than Parathemisto spp. (Table 5-2).

During the time of evacuation as food was digested, the dry/wet weight ratio of stomach contents did not increase much over time (Table 5-2), although the increase was significant in 1989, indicating some extraction of liquid components from food items in stomachs. Energy content of digesting Calanus, in the 1990 experiment, decreased about 0.53 % · d^{-1}, although this reduction was not significant (p = 0.167).

After digestion in the stomach, the chyme is evacuated via peristaltic contractions through the pylorus to the upper intestine where it is further digested and assimilated (Dos Santos and Jobling 1991). In Arctic cod there was a distinct separation between stomach and intestine. A pyloric sphincter was located in a small extension of the stomach, at about 60 % of its length measured from the oesophagus. Immediately behind the pyloric sphincter 17-37 pyloric caeca (mean ± SE, 28 ± 0.6), were located on the duodenum. The intestine was organized in a single coil and consisted of a small (or upper) intestine and a colon section (lower intestine), which could be identified as separate sections since the colon had a slightly wider diameter. Lengths of intestine and pyloric caeca were directly proportional to the fork length of the fish (Table 5-3). The intestine was about half the length (51 %) of the fish, but coiling made it only half as long (26 % of fish length). The colon section was about one-third of the fish length, or two-thirds of the intestine length.

Field samples of small and large Arctic cod showed diurnal variation in stomach fullness in July (Figure 5-3a). Mean stomach fullness varied from 0.7-2.8 % for small fish and 2.4-5.2 % for large fish, with low fullness during the day and high fullness during the night. The mean of these values indicated that relative stomach fullness was only 16 % during the day, and up to 44 % (large fish) and 58 % (small fish) during the night (Figure 5-3b). However, during subsequent sampling periods in August, diurnal variation in stomach fullness was almost non-existent (Figure 5-3c). Stomach fullness varied between 0.9-

1.4 % (27 % of maximum) in early August, and between 2.4-5.2 % (37 % of maximum) in late August. The average level of relative stomach fullness for small and large fish was 32 %.

Estimated daily ration for small fish varied between 0.017-0.029 g · d^{-1} or 0.4-0.6 % body weight · d^{-1}, with a mean of 0.023 g · d^{-1} or 0.5 % body weight · d^{-1}(Table 5-4). Large fish had a higher daily ration, 0.572 g · d^{-1} or 1.11 % body weight · d^{-1}, which was similar to half-time evacuation rates (over 24 h).

Discussion

Most gastric evacuation studies have applied exponential decrease models (e.g., Tyler 1970; Elliott 1972; Persson 1979, 1981; Dwyer et al. 1987), although linear functions have also been used (e.g., Panadian 1967; Lambert 1986; Jobling 1987). Jobling (1986, 1987) showed that the mathematical expression having the best fist to empirical values may vary with species, food type and experimental conditions. Jobling (1986) predicted that exponential functions would best describe the emptying of small, easily digestible, low energy food particles from the stomach, whereas linear expressions would give better fits when food consisted of high energy, large-sized particles. The rate of gastric evacuation is also dependent on feeding history prior to experiments, since we found that exponential regressions gave the best fits for gastric evacuation when fish were fed regularly prior to the experiment, whereas evacuation rates were slower and better fitted by linear functions when fish were starved prior to satiation feeding. Tyler (1970) also indicated that starving fish prior to experiments may slow down digestion rates. The exponential model is applicable to non-schooling fish in the wild, since their stomachs generally contained food when fish were sampled during the open water season (Hop et al., in press), whereas the linear model could be applied to schooling Arctic cod, which only feed occasionally on temporarily abundant zooplankton resources (Hop et al., in press). We found no significant difference

in gastric evacuation rates among size-groups of fish, and evacuation rates were not dependent on food type.

Evacuation rate parallels digestion rate when the dry/wet weight ratio of the stomach contents is constant over the time of evacuation, and passage of stomach contents to the intestine then occurs as rapidly as food is digested, with little build-up or removal of liquids from the stomach (Tyler 1970). This was supported by our experiments, in which the dry/wet weight ratio did not change much over time. In addition, digestive processes did not significantly affect caloric density of stomach contents in Arctic cod. We found a small, non-significant decrease in stomach energy content during evacuation, which was similar to findings by Kolok and Rondorf (1987) for gastric evacuation in chinook salmon (Oncorhynchus tshawytcha Walbaum, 1792).

Dietary energy content can influence gastric emptying, with energy rich food being emptied at a slower rate (Grove et al. 1978). Jobling (1988), however, pointed out that gastric emptying in cod was relatively insensitive to changes in dietary energy content. In our experiment the caloric density of Calanus spp. was significantly higher than that of Parathemisto spp., but evacuation rates were not significantly different. The difference in energy content of the two prey was probably too small to influence on evacuation rates significantly.

Gastric evacuation half-times for Arctic cod were considerably longer than those reported for other cod species, although none of those studies were conducted at sub-zero temperatures. For instance, Tyler (1970) found a considerably shorter evacuation half-time (13 hours) for juvenile Atlantic cod at 2 °C. However, these fish were not fed to satiation in this experiment (wet weight of food was 0.18 % of body weight), and the resulting stomach evacuation rates are therefore not directly comparable to our experiments.

Increased meal size generally results in increased evacuation rates (e.g., Kitchell and Windell 1968; Tyler 1970), but may also result in increased evacuation time (Jobling 1989). This implies that a given percentage of the

meal may be digested in the same time for different meal sizes (Elliott 1972), although other workers have found that a larger meal, while evacuated at a faster rate, generally has a longer half-time (Beamish 1972).

The maximum quantities that Atlantic and Pacific cod (Gadus macrocephalus Tilesius, 1810) will hold in their stomach, 5.5 and 4.7 % of body weight, respectively (Tyler 1970; Paul et al. 1990), was considerably less than maximum stomach fullness for Arctic cod. This may partly explain the relatively slow evacuation rates (as % body weight · d^{-1}) relative to those found for the other cod species. In our experiment fish were fed to satiation, but there will be fish that feed less than the maximum possible, so that the mean stomach weight at the start of each experiment will be lower. We found that maximum stomach fullness increased with the size of the fish, and this relationship indicated that the small, medium and large fish in our experiment would have fed to the maximum at stomach fullness 7, 9 and 13 %. In our evacuation experiments the smallest and medium sized fish therefore fed close to maximum levels, whereas the largest fish were below maximum stomach fullness.

There is some evidence that initial meals are evacuated more rapidly when followed by additional food (Fange and Grove 1979; Paul et al. 1990). In our 1990 experiment evacuation half-time of the initial meal was somewhat shorter when the fish were fed subsequently, although the evacuation rates were not significantly different. Subsequent meals tend to be "stacked up" in stomachs of Atlantic cod (Dos Santos and Jobling 1991), which may explain the limited effect of subsequent meals, and also why the two prey types fed sequentially in our 1990 experiment did not mix much in stomachs. Our preliminary experiment with chromic oxide, showed that this technique works for determining gut passage time when fish are fed multiple meals, but this experiment was terminated after five days, and only a fraction of the fish had passed the substance through within that time.

Gastric evacuation rates (R) for Eurasian perch (Perca fluvatilis L.) have been determined over a wide range of temperatures, down to 5 °C (Persson 1979). The relationship between R and temperature was described by an exponential function (Elliott 1972):

$$R = a\, e^{bT}$$

where a and b were empirically determined constants (a = 0.0182, b = 0.140), and T was temperature. Extrapolating this relationship beyond its original range to -1.42 °C would give an instantaneous rate of evacuation of $1.491 \cdot 10^{-2}$ (h^{-1}) which was similar to the rates we found for small and large Arctic cod fed Calanus spp. This may indicate that Arctic cod do not have special cold-adapted digestive enzymes.

The slow gastric evacuation rates observed for Arctic cod were probably temperature dependent, with digestive processes being slow at sub-zero temperatures. These slow rates would have implications for stomach fullness observed in field samples and daily consumption rates. If fish fed close to maximum, one would predict that slow evacuation rates would preclude diurnal variation in stomach weights. However, the observed diurnal pattern in stomach fullness of small and large Arctic cod in late July suggested a diurnal variation in feeding activity. Stomach fullness of field samples indicated that Arctic cod stomachs only contained 32 % of maximum fullness, and therefore diurnal pattern could be detected. Then mean stomach fullness after sustained feeding to satiation also seems to be much lower than maximum stomach fullness (after being fed once to satiation on an empty stomach), since stomachs dissected from fish fed to satiation in experiments also contained about 30 % of maximum (Hop et al., in prep.). Fish in the field may have been feeding at near a sustained satiation level, on average.

If one assumes a steady state in which evacuation rates equal consumption rates, our experiments indicated consumption rates of 1-2 % of body weight $\cdot$ d^{-1} at half-time (± 12 h), and about 1.5 times that for full stomachs (within the first 24 h). Daily rations for field samples of large fish

were close to half-time evacuation rates (± 12 h) and less than that for small fish, indicating low daily rations for non-schooling juveniles. Maximum daily rations determined for small fish in controlled feeding experiments were similar to our half-time evacuation values for small fish (Hop et al., in prep.). Sporadically feeding fish (i.e., schooling individuals) likely have mean daily rations even below 0.7 % · d^{-1} evacuation rate found in this study. Based on multiple meal experiments, Smith et al. (1989) postulated that walleye pollock (Theragra chalcogramma Pallas, 1814) were adapted either to feed at moderate levels on a continuous basis, or to ingest very large meals when food supply was scarce. The same may apply to non-schooling versus schooling Arctic cod. Smith et al. (1989) also pointed out that gastric evacuation and feeding periodicity may be linked, with slower evacuation rates associated with fish that fed infrequently. Retaining food in the intestinal system will also likely increase assimilation efficiency, which is high (80 %) for Arctic cod (Hop et al., in prep.). This could be important for Arctic cod, e.g., to minimize weight loss during schooling.

Slow gastric evacuation rates at sub-zero temperatures seem to limit daily food intake, which will subsequently lead to slow growth rates for Arctic cod in high arctic waters (Hop et al., in press). However, all bodily functions, including metabolism, are slow at low ambient temperatures. Slow growth rates may then also limit the maximum size (< 30 cm) of a fish that has a maximum life span of seven years (Bradstreet et al. 1986; Hop et al., in press).

Table 5-1. Results of gastric evacuation experiments for Arctic cod (mean fork length and weight ± SE) fed different prey. Y-intercepts (W_o) and evacuation rates (R) are indicated for exponential (1989) and linear (1990) regressions, with respective evacuation half-times. Daily evacuation rates are indicated for the first 24 h and at half-time (± 12 h).

Prey	n	Temp. (°C)	Mean FL (mm)	Mean WT (g)	Wo (%)	R (x 100)	r-squared	Half-time (h)	Evacuation rate (24 h) (% · d^{-1})	Evacuation rate (24 h) (g · d^{-1})	Evacuation rate (24 h) (kJ · d^{-1})	Evacuation rate (half time) (% · d^{-1})	Evacuation rate (half time) (g · d^{-1})	Evacuation rate (half time) (kJ · d^{-1})
1989														
Calanus	34	-1.42±0.07	95.6±1.0	6.18±0.19	12.16	-1.388	0.828	50	3.45	0.21	1.504	2.03	0.13	0.921
Calanus	35	-1.42±0.07	188.1±1.9	46.39±1.34	6.32	-1.408	0.793	49	1.81	0.84	6.018	1.08	0.50	3.543
Parathemisto	34	-1.42±0.07	99.7±1.5	7.01±0.33	8.43	-1.924	0.803	36	3.12	0.22	0.953	1.97	0.14	0.602
Parathemisto	38	-1.42±0.07	186.6±2.2	43.58±1.44	7.64	-0.999	0.516	70	1.63	0.71	3.076	0.91	0.40	1.706
1990														
Calanus	60	-0.49±0.08	145.6±0.7	21.07±0.36	9.25	-2.887	0.435	160	0.69	0.15	1.231	0.69	0.15	1.187
Calanus/Parathemisto	60	-0.49±0.08	146.8±0.8	21.57±0.41	7.76	-2.684	0.508	146	0.64	0.14	1.133	0.69	0.14	1.096

Table 5-2. Ratio (± SE) of wet/dry weight (%) of zooplankton prey in Arctic cod stomachs (n). Linear regression parameters (r^2 and p) indicate whether the dry/wet ratio increased significantly during time of digestion.

Feed	n	Dry/Wet (%)	r-squared	p
1989				
Calanus	68	24.4±0.3	0.167	0.0005
Parthemisto	73	20.9±0.3	0.069	0.0243
1990				
Calanus [a]	54	28.2±0.4	0.034	0.1982
Calanus [b]	54	27.8±0.3	0.002	0.7214

[a] Single meal experiment
[b] Multiple meal experiment

Table 5-3. Mean lengths (± SE) of intestine sections as percentage of fork length of Arctic cod (FL range 123-267 mm). Linear regressions (p = 0.0001) indicate relationships between intestine section length (GL) and fork length (FL).

Section	Mean length (% of FL)	Regression	r-squared
Pyloric caecum	6.8±0.3	GL = 0.074 * FL - 1.072	0.777
Coiled intestine	26±0.5	GL = 0.262 * FL - 0.404	0.717
Uncoiled intestine	51.3±0.7	GL = 0.609 * FL - 14.691	0.857
Colon	33.4±1.3	GL = 0.419 * FL - 12.208	0.811

Table 5-4. Estimates of daily ration for small and large Arctic cod from Resolute Bay, N.W.T., 1989. Estimates of daily ration are based on mean daily stomach fullness in the field and instantaneous stomach evacuation rates determined in the laboratory; see Methods for details.

Date (1989)	n	Mean fish wt. (g)	Empty stom. (%)	Estimated daily ration ($\% \cdot d^{-1}$)	($g \cdot d^{-1}$)	($kJ \cdot d^{-1}$)
Small fish						
29-30 July	45	4.5	4.4	0.53	0.024	0.172
9-11 August	98	4.2	11.2	0.40	0.017	0.122
30 Aug.-1 Sept.	117	4.9	12.8	0.59	0.029	0.208
Mean		4.5	9.5	0.51	0.023	0.167
Large fish						
29-30 July	86	51.0	1.2	1.13	0.579	4.148

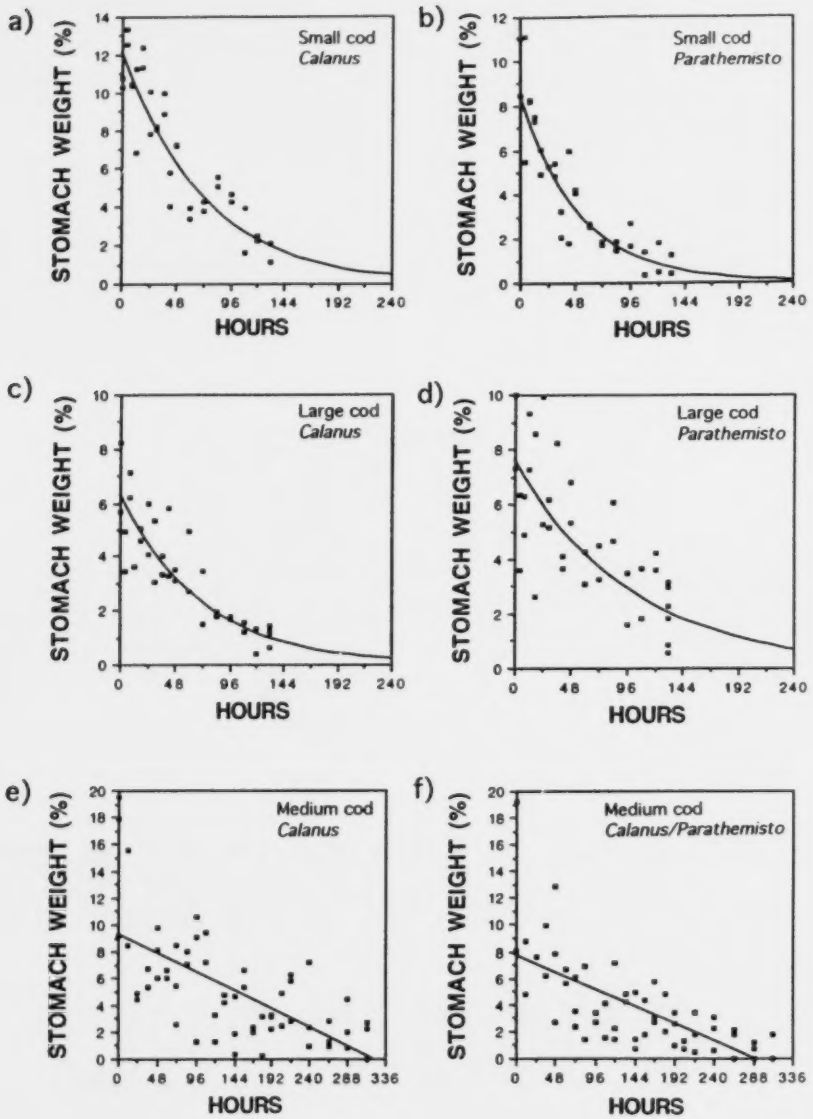

Figure 5-1. Gastric evacuation, as change in stomach fullness over time, for different size-groups of Arctic cod fed live zooplankton (see Methods). All weights are wet weights, and mean fish weight (± SE) of size groups used in experiments are indicated below.

a) Small fish (6.18 ± 0.19) fed Calanus.

b) Small fish (7.01 ± 0.33) fed Parathemisto.

c) Large fish (46.39 ± 1.34) fed Calanus.

d) Large fish (43.58 ± 1.44) fed Parathemisto.

e) Medium fish (21.07 ± 0.36) fed Calanus.

f) Medium fish (21.57 ± 0.41) fed Calanus first and Parathemisto subsequently.

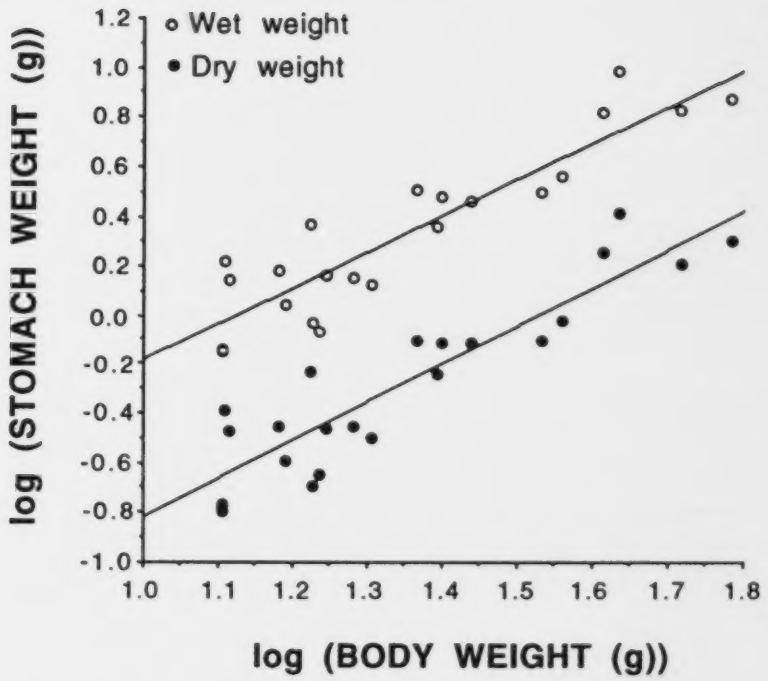

Figure 5-2. Relationship between maximum stomach content weight (wet and dry) and wet body weight (whole body - stomach content) determined for Arctic cod (n=22) fed to satiation. The lower quartile of the original data have been trimmed to obtain relationship for maximum stomach weight (i.e., fish that fed below maximum stomach fullness have been eliminated).

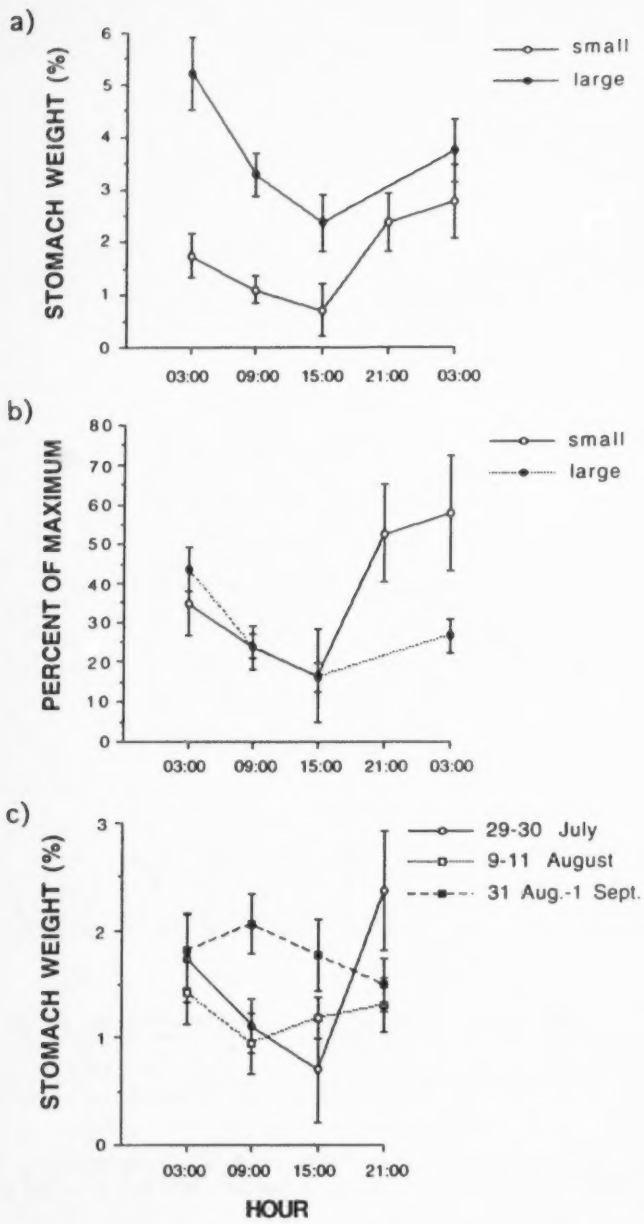

Figure 5-3. Diurnal variation in mean stomach fullness of Arctic cod in Resolute Bay, 1989. Empty stomachs are included in the mean values (± SE).

a) Mean stomach fullness of small (mean wt. 4.5 g) and large (mean wt. 51.0 g) fish, 29-30 July.

b) Mean relative stomach fullness (see Methods) for small and large fish, 29-30 July.

c) Mean stomach fullness of small (mean wt. 4.5 g) fish on three dates, July-September.

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CHAPTER 6

Feeding energetics of Arctic cod (*Boreogadus saida*) at low temperatures

A version of this chapter will be submitted for publication, as a manuscript co-authored with William M. Tonn and Harold E. Welch. Contribution no. 25 from the Resolute Marine Laboratory.

Introduction

Arctic cod (Boreogadus saida Lepechin, 1774) is a key component in the high arctic marine food web (Bradstreet et al. 1986; Hobson and Welch 1992; Welch et al. 1992), with annual predation by sea birds and marine mammals estimated to be in the order of 148, 000 metric tons in the Lancaster Sound Region of the Canadian High Arctic (Welch et al. 1992). Estimates of the energy flow through parts of the food web have been made, including preliminary values for annual ingestion and growth by Arctic cod (Welch et al. 1992). However, there is presently a major discrepancy between estimates of Arctic cod abundance/production and total annual predation on cod, with the estimates of cod abundance being far too low to account for the production consumed by marine mammals and seabirds (Welch et al. 1992). In addition, better estimates of energy flow though Arctic cod are needed to properly assess production at this intermediate trophic level. An initial step in this process is to establish daily consumption and growth rates of Arctic cod, and subsequently develop an energy budget for this species.

In this study we have used an experimental approach to feeding energetics of Arctic cod at low temperatures. Field estimates of daily consumption rates are generally not very accurate, since it is impossible to measure consumption rates directly. They can be inferred from measurements of gastric evacuation rates and mean stomach fullness (e.g., Bajkov 1935; Jobling 1982; Dwyer et al. 1987; Hop and Tonn, in prep.), but the variability in stomach fullness of Arctic cod is high (Hop et al., in press). In experimental studies daily rations can be controlled and resulting growth rates monitored, which makes it possible to calculate growth efficiencies directly. Many studies of growth efficiencies based on controlled food intake exist for other gadid species; Atlantic cod (Gadus morhua L.) (Edwards et al. 1972; Jones and Hislop 1978; Jobling 1988), Pacific cod (Gadus macrocephalus Tilesius, 1810) (Paul et al. 1990 a) and walleye pollock (Theragra chalcogramma Pallas, 1814) (Smith et al. 1986; Paul

et al. 1990 b). However, only limited information on feeding energetics is available for Arctic cod. Jensen et al. (1991) measured growth and daily consumption rates for a group of Arctic cod from the Barents Sea, that were fed peeled shrimp at -1.0 °C. Our study differed in that it used live arctic zooplankton fed to individual fish, at ambient temperatures in the Canadian High Arctic. Holeton (1974) determined respiration rates for different sizes of Arctic cod at a single temperature (-1.5 °C), whereas Hop and Graham (in prep.) included different temperatures and the effect of acclimation and food intake. The only complete energy budget that exists for a polar marine fish is that of the Antarctic icefish (Notothenia neglecta Nybelin, 1951) (Everson 1970).

The present study is the first to establish an energy budget for an arctic marine fish, where Consumption = Growth + Respiration + Waste losses (Brett and Groves 1979). Little experimental work, apart from the study by Jensen et al. (1991), has been done on feeding energetics of arctic marine fishes presumably because of limited laboratory facilities that can sustain fish at low temperatures (close to 0 °C) for sufficient time periods. In this paper we report daily rations and growth rates of Arctic cod based on data from controlled feeding experiments on individuals and groups fed different diets and rations. Our experiments were carried out at the Resolute Bay Marine Laboratory, Department of Fisheries and Oceans, Canada, in Resolute, N.W.T. (75°40' N , 95° W), and we also report results from one set of experiments conducted at the Ocean Sciences Center, Memorial University of Newfoundland, in St. John's, Newfoundland.

Materials and Methods

Arctic cod were collected by trap nets from Resolute and Allen Bays, on the south coast of Cornwallis Island, N.W.T. Three collections were made, one each for experiments in 1988 (variable size, fork length 68-254 mm),1989

(small size, fork length 80-101 mm), and 1990 (medium size, fork length 108-128 mm).

1988 experiments

Fish, collected in mid August, were kept a few days in the Resolute Marine Laboratory, before being shipped to St. John's, Newfoundland, on 24 and 31 August. Fish were put in large, clear plastic bags that contained about 5 L of water on the bottom, with 5-10 individuals per bag, depending on fish size. The bags were filled up with oxygen and placed inside 90 L insulated coolers that had a layer of crushed ice on the bottom. Transit time was about 24 hours, during which the temperature had increased < 2 °C, and there was no mortality. Upon arrival at the Ocean Sciences Center fish were put into two cooled 380 L holding tanks containing seawater (29 ‰ salinity). The temperature was 10-12 °C when the first shipment of 21 fish arrived, but was subsequently brought down to about 0 °C within a few days. Only a few mortalities resulted from this temperature shock, indicating that Arctic cod are quite tolerant to acute temperature effects (Hop and Graham, in prep.). The second shipment of 65 fish experienced no such temperature shock. The fish were acclimated to the tanks for about 1.5 months and became accustomed to feeding on chopped frozen capelin (Mallotus villosus Müller, 1777) fillets within 2-3 weeks; fish were fed at below satiation level on alternate days until the experiment started.

The experimental set-up consisted of four glass aquaria (37.5 L) inside two reservoir tanks. Each glass aquarium was divided by perforated (3 mm PVC screen) walls into four compartments with various volumes of water (large, 10 L; medium, 8 L; small, 6 L) to accommodate different sized fish. Experimental compartments were divided equally between the two reservoir tanks, and one additional compartment (18.5 L) in each reservoir tank contained a group of twelve fish. A small pump inside each reservoir tank supplied water (about 1 L $\cdot$ min^{-1}) to individual compartments through a branched hose. Water overflowed back to the reservoir, through screens (1.5 mm mesh) near the upper edge of

each glass aquarium. Ambient saltwater supplied to each reservoir tank was 0.5-1.0 L · min^{-1}. A screened frame covered the glass aquaria, and each reservoir tank was covered by an insulated lid. Fish were thus kept in darkness except during cleaning and feeding (3-4 hours · day^{-1}). Temperature was monitored daily during the experiment, and the salinity was determined bi-weekly

The experiments, which lasted 56 days (mid October - mid December), included four treatment groups; individual fish fed maximum (n=14) and reduced rations (n=12), and groups of fish (fork length range = 150-199 mm, marked individually with combination fin clips) fed maximum rations (n=12), and maximum rations during the first month followed by starvation (n=12). Fish on maximum ration were fed to satiation, whereas fish on reduced ration were fed rations which decreased by half every two weeks (2, 1, 0.5, 0.25 % of body weight). Freshly thawed and chopped capelin fillets were weighed (0.01 g) prior to feeding, which occurred on alternate days, and excess food was removed from the compartments, blotted on tissue paper and re-weighed. Samples of capelin fillets (10 g) were taken every four days throughout the experiment. Dry weight (%) and energy content of capelin did not change significantly ($p = 0.540$) throughout the experiment. All fish (anesthetized in MS-222) were measured (mm) and weighed (0.01 g) five days after the feeding schedule had been started (day 0), and then every two weeks until the experiment was terminated (day 56).

Faecal matter was carefully siphoned out of individual compartments daily into small (45 mm wide) hexagonal trays, and water was decanted. Faeces were dried for 24 h at 60 °C, pooled for two days of collecting, and weighed (0.001 mg).

At the end of the experiment, fish were frozen and later dissected with the following tissues weighed: carcass, liver, gonads and intestines (less stomach contents). Arctic cod (n=100), collected by trawl from Resolute Bay in

late July - August, and dissected in the same manner, served as standards. All tissues were dried at 60-70 °C to constant weight (4-5 days).

The caloric density of dried, homogenized samples (1.0 g) of tissues and faecal matter were determined by adiabatic bomb calorimetry (Adiabatic bomb calorimeter 1241) with results expressed in Joules (1 calorie = 4.1855 J). The procedure was standardized with benzoic acid pellets (n=10) of known energy content (26,444 $J \cdot g^{-1}$), and resulting energy values were corrected for combustion of fuse wire and formation of nitric acid. In addition, total protein was determined by the Kjeldahl nitrogen procedure (Bradstreet 1965), and total lipids by methanol/chloroform extraction (Folch et al. 1957).

1989 experiments

Fish, collected during 14-20 July, were kept in flow-through holding tanks with seawater of about 30 ‰ salinity, in the Resolute Marine Laboratory for two weeks, during which time they became conditioned to feeding on live arctic zooplankton, adult copepods (Calanus spp., predominately C. hyperboreus and C. glacialis) and juvenile amphipods (Parathemisto spp., predominately P. libellula). A uniform length group of fish that were in good condition (with no external damage, and normal feeding behavior) were selected for the experiments.

The experimental tanks, designed for feeding experiments on individuals, consisted of two reservoir tanks with individual boxes. The fiberglass reservoir tanks were 180 cm long, 45 cm wide and 30 cm deep, and ten plexiglass boxes, with walls of 1.5 mm black screen, were glued to the bottom of each tank. Boxes were 11.5 cm wide, 23 cm high, and of variable length (20-40 cm). In experiments with small fish, all boxes were adjusted to the same length (20 cm) by adding screened walls. Before experiments started, all fish were conditioned for one week to feed individually in these boxes. Screens, covering the entire tank set-up, prevented fish from jumping out.

Water was pumped from Resolute Bay at 5-6 m depth, and was filtered through a screen (0.8 mm) before entering a settling tank (200 L). A pump (Fluval 403), with ceramic pre-filters and foam filters, pumped water from the settling tank into each of the reservoir tanks. Water flowed into each reservoir tank at one end through a perforated pipe, and an overflow pipe at the other end kept the water level at 21 cm. Sediments and particles in the settling tank and foam filters were removed daily. Temperatures in the tanks, monitored daily, were generally within 0.2 °C of ambient water temperature. Illumination was not controlled, although the lab was normally dark between 22:00-09:00 hours, except that windows close to the tanks provided some natural lighting.

The experiments, which lasted 48 days (early August - end of September), contained five treatment groups. One experimental group (n=10) was fed Calanus spp. and one group (n=10) Parathemisto spp. daily. Within each group half of the fish were fed to satiation, with the other half being fed reduced rations, at approximately maintenance levels. After 24 days these rations were lowered from two to one prey daily. In addition, a starvation group (n=8) was included. Fish were measured and weighed every 12 days, and faecal matter was collected as described previously. Dried faecal matter from each fish was pooled for each 12-day period before being weighed (0.1 mg).

Each fish in its box was fed a number of live zooplankters. Satiation was assumed when a fish refused five times to take additional individual zooplankters delivered by a pipette. Zooplankton remaining in each box after each feeding were removed and counted. We attempted to use single size-classes of Calanus or Parathemisto throughout the experiment, and lengths and weights of prey were periodically measured. Zooplankton was obtained every 3-4 days from Resolute Passage, with a large plankton net (1 m diameter, 0.9 mm mesh), towed horizontally at various depths. The plankton was sorted through screens into the two prey groups and kept in flow-through, aerated holding tanks (200 L). Samples of plankton were counted, weighed, dried before

caloric densities were measured by bombing, although potential changes in caloric values of zooplankton collections over time were not determined.

Arctic cod (n=15) were also collected by trawl from Resolute Bay on 9 August, close to the time when the feeding experiment started. These fish served as standards for caloric determinations of experimental fish. Caloric density, total lipids and total protein of zooplankton, fish and faecal matter were determined as previously described.

1990 experiments

These experiments were similar to the 1989 experiments, with the following differences. Fish used in experiments were larger, and they were fed only Calanus spp.; both numbers and weight (0.1 mg) of daily individual rations were determined. The experiments, which lasted 36 days (mid August - late September), contained three treatment groups (n = 10 per group), and included maximum (satiation) and reduced (close to maintenance) rations, and starvation. Reduced ration levels were three Calanus daily. Two fish in the maximum ration treatment were excluded from growth calculations, since they rarely feed during the initial period and thus lost weight.

The experimental set-up was expanded to four reservoir tanks with individual boxes inside. The filter system was improved over 1989; the water was additionally filtered through a 0.55 mm screen and a 10-cm thick filter-floss mat (replaced weekly), placed inside a 50 L tub on top of each settling tank. The additional filtering was rendered necessary since it was noted that small harpacticoid copepodites, occurring in September, would pass through the previous filter-system.

Energy budgets

Daily rations were determined as the mean number of individual zooplankters, or the wet weight of zooplankton or capelin fillets, consumed per day. Growth for a slow growing fish, such as Arctic cod, was approximately

linear over the experimental periods, and we therefore used linear growth rate models rather than instantaneous models (Jobling 1983). The absolute (G_1) and relative (G_2) growth rates determined as:

$G_1 = (W_2-W_1)/(t_2-t_1)$ and $G_2 = G_1/W_1 \cdot 100$

where W_1 and W_2 denote wet weight (g) at time t_1 (day 0) and t_2 (last day of experiment), respectively, assuming that growth is approximately linear between t_1 and t_2 (Busacker et al. 1990).

Parameters in the subsequent equations were based on values converted to energy equivalents. The energy budget (Brett and Groves 1979) for Arctic cod in experiments was considered to be:

$C = G+R+F+U+Z$

where C = consumption, G = growth, R = respiration + specific dynamic action, (SDA), F = egestion (faeces), U = excretion (of ammonia), and Z = activity and other energy unaccounted for. Budget components (right side of equation) were expressed as percentage of consumption.

Gross growth efficiency (GGE), the capacity to convert food into flesh (Ivlev 1939; Welch 1968) was:

$GGE = G/C \times 100$

Assimilation efficiency (AE; Welch 1968) was:

$AE = (G+ R)/C \times 100$

and net growth efficiency (NGE; Ivlev 1939; Welch 1968) was:

$NGE = G/(G+R) = G/A$, where A was assimilated energy.

Consumption (C) was determined from daily rations and energy contents of food.

Growth (G) in wet weight was converted to energy equivalents based on the dry/wet weight ratio and mean caloric content of dried Arctic cod. Change in energy content of experimental fish was accounted for.

Respiration (R) was obtained from a separate study on oxygen consumption by starved and fed Arctic cod (Hop and Graham, in prep.). The values used here were routine metabolic rates, determined as oxygen

consumption rates for short-term acclimated (2 weeks) fish at ambient temperatures (-1.5 to 0.5 °C) at the Resolute Marine Laboratory. Rates were adjusted to the mean temperature and fish-size in each of our experiments, based on relationships between oxygen consumption and temperature (Hop and Graham, in prep.) and size (Holeton 1974). Oxycalorific coefficients (Q_{ox}) were determined based on the substrate being respired; Q_{ox} = 13.72 for lipids, and 13.36 for protein (Brett and Groves 1979; Brafield 1985). Starved Arctic cod probably use energy stored in the large liver for respiration. A lipid:protein ratio of 14.94 in the liver results in Q_{ox} =13.70 J · mg^{-1} O_2. Respiration energy in fed fish was assumed to originate from the diet. The lipid:protein ratio was 0.24 for capelin, 1.62 for Calanus and 0.65 for Parathemisto, which resulted in Q_{ox} of 13.43, 13.58, and 13.50 J · mg^{-1} O_2, respectively. Since fish were individually confined to boxes, they were generally not very active. We did not account for activity, but attempted to estimate its magnitude based on maintenance energy (i.e, budget where G = 0) in the 1990 experiment.

Egestion (F) was calculated from the energy content of faecal matter collected daily from fish in experiments, and from other fish fed the same food items (to get sufficient quantity for caloric determinations).

Excretion (U) was determined from ammonia in water samples, taken after 2-3 h, from closed chambers containing juvenile Arctic cod that were starved or fed krill (Euphausia pacifica), having a mean energy content 4.897 kJ · g^{-1} wet weight. Samples were kept in the dark on ice until analyzed. Total ammonia (NH_3 + NH_4^+) was analyzed in diluted (1/10) samples on a Technicon Auto Analyzer according to the procedure of Stainton et al. (1977). We used 20.5 J · mg^{-1} excreted ammonia as conversion value (Brafield 1985).

Results

Temperature

Temperatures in the three experiments were generally within ± 1.0 °C of zero (Figure 6-1). In the 1988 experiment the daily temperature was relatively constant, 0.10 ± 0.02 °C (mean ± SE). In 1989 and 1990 temperatures fluctuated more and dropped slightly over the course of the experiments, reflecting ambient changes. Fluctuations were generally caused by wind mixing of the water column, and the temperature drop towards the end of the season resulted from surface cooling (Hop et al., in press). Mean daily temperatures (± SE) were 0.01 ± 0.10 °C in 1989 and -0.18 ± 0.11 °C in 1990.

Growth rates

In the 1988 experiment, with various sizes of fish at maximum rations, both absolute (G_1) and relative (G_2) growth rates depended on the initial weight or length of fish. Small fish had lower absolute rates of growth by weight than larger fish, with rates stabilizing for fish > 20 g (Figure 6-2a), although small fish had higher relative rates of growth than larger fish (Figure 6-2b). Small fish grew mostly in length, and had higher absolute and relative growth rates by length than large fish (Figure 6-2c, d). Growth within different size-groups was approximately linear in all experiments thus we used linear growth models in calculation of rates of growth by weight. In the 1988 experiment with maximum rations, large individuals grew at a faster absolute rate (147-150 mg $\cdot$ d^{-1}) than smaller fish (53 mg $\cdot$ d^{-1}) (Table 6-1, Figure 6-3a). Reduced rations gave reduced growth over time as rations declined (Figure 6-3b). Growth became zero or slightly negative after 28 days at a ration of 0.5 % body weight $\cdot$ d^{-1}, indicating that this ration was close to maintenance (zero growth). The smallest fish showed little change in growth with ration size, although these small rations were difficult to weigh accurately. In the group feeding experiment, fish grew somewhat faster (177-241 mg $\cdot$ d^{-1}) than in experiments

with individuals (Table 6-1, Figure 6-3c). Starved fish (group 2) lost 150 mg · d^{-1} during the first week of starvation, probably because stomach contents were still being digested and evacuated (Hop and Tonn, in prep.), and then 81 mg · d^{-1} during the next 20 days (Table 6-1, Figure 6-3c).

Feeding experiments in 1989 and 1990 showed that growth was affected by both ration size and type. Fish fed maximum rations of Calanus in 1989 had faster growth rates (56 mg · d^{-1}) than similarly-sized fish fed Parathemisto (38 mg · d^{-1}) (Figure 6-4a). Larger fish fed maximum rations of Calanus in 1990 had slightly higher absolute growth rates (63 mg · d^{-1}) and lower relative rates than the smaller fish in 1989 (Table 6-1, Figure 6-4a, b). Reduced rations were adjusted to approximate maintenance ration, and gave close to zero growth (1989) or slight weight loss (1990). The starvation groups lost weight both years, although both absolute and relative weight loss was greater in 1990 (43 mg · d^{-1}, or 0.36 % · d^{-1}) than in 1989 (7 mg · d^{-1}, or 0.13 % · d^{-1}). Low weight loss in 1989 was likely related to insufficient filtering of inflowing water (see Methods).

Maximum daily rations

In 1989 daily rations were determined based on numbers of prey consumed and mean (± SE) weights of individual Calanus (11.00 ± 1.65 mg) and Parathemisto (20.49 ± 1.28 mg), in samples of 250-650 individuals, whereas rations were weighed in 1990. Maximum daily rations (MDR) of Calanus was 10 individuals (mean length 6.5 mm) for by small fish, and 18 individuals (mean length 5.0 mm) for larger fish, corresponding to daily rations of 99 and 168 mg, respectively (Table 6-1). Maximum daily ration of Parathemisto for small fish was 5.5 individuals (mean length 12 mm), corresponding to 113 mg, which was similar to the ration of Calanus. There was a significant relationship ($p = 0.0001$) between numbers of Calanus consumed (MDR_n) and fish weight for the 1989 and 1990 experiments combined (Figure 6-5a). Given a significant relationship ($p = 0.0001$, $r^2 = 0.985$) between numbers (MDR_n) and weights

(MDR_w) of Calanus consumed in 1990, MDR_w also changed with fish weight. However, only a limited size range of fish was used in the 1990 experiment (Figure 6-5b). Therefore, to establish a significant ($p = 0.0001$) relationship between MDR_W and fish weight, we used ration weights of capelin fillets from the 1988 experiment (Figure 6-5b).

Maintenance ration

Daily rations for fish fed on reduced (near maintenance) rations were 10-44 mg $\cdot$ d^{-1} (Table 6-1). We determined the maintenance ration of Calanus by regressing mean daily ration against mean absolute growth rate (G_1) for individual fish (mean weight 12 g) in the 1990 experiment. Daily maintenance ration was 60.2 mg (583.7 J) of Calanus (Figure 6-6a), which was equivalent to 5.7 individuals per day. This maintenance ration was equivalent to 0.5 % body weight $\cdot$ d^{-1}, which was similar to that indicated in the experiment with declining rations over time (Figure 6-3b). However, to also maintain the energy content of a 12 g Arctic cod, more energy (716.3 J) was needed (Figure 6-6b), which corresponded to 73.8 mg (0.6 % body weight) or 7.2 individual Calanus per day.

Energy contents

The energy content of food affected growth rates of small fish fed at maximum rations. The fastest growth rates resulted from Calanus, which had a higher energy content than capelin fillets and Parathemisto (Table 6-2). The high energy content of Calanus was due to a high lipid content (Table 6-2). Parathemisto contained less energy per unit weight because of a lower lipid content and the presence of a thicker exoskeleton. Capelin fillets contained mostly protein, which contain less energy than lipids (Brafield 1985). Arctic cod store energy as lipids (mainly triglycerides) in the large liver (Table 6-2), which was most notable in adults that use this energy in gonad production (Hop et al., in prep.). The overall energy contents of males and females were

similar, and slightly higher than that of juveniles (Table 6-2). Overall, Arctic cod contained more protein than lipids, since carcass (low in lipids) constituted a much higher proportion (77.5 %) of the total weight than liver (9.2 %).

The energy content of faecal matter was highest for capelin and lowest for Parathemisto, while energy contents of faecal matter from wild fish were intermediate of faeces from Calanus and Parathemisto diets (Table 6-3). The amount of dry faecal matter recovered daily in experiments varied between 1-5 $mg \cdot d^{-1}$, with Parathemisto diets giving the highest daily amounts because of poorly digestible chitinous exoskeletons (Table 6-1). Besides, faecal matter of zooplankton diets contained mostly protein (lipid:protein ratio 0.1-0.5), indicating that lipids were predominately assimilated. Faecal matter of capelin diets contained relatively more lipids (lipid:protein ratio 3.3), which explained their higher energy contents, but indicated poorer assimilation of lipids. However, lipids in zooplankton and capelin are different in that arctic Calanus spp. contain high amounts of wax esters (Lee 1974), whereas capelin contains mainly triglycerides (Montevecchi and Piatt 1984).

Fish fed to satiation increased in weight, but they also changed in energy content; both have to be considered when accounting for energy assimilated into growth. Fish fed on capelin diets added weight but lost energy from tissues, whereas fish fed Calanus added energy content and fish fed Parathemisto changed little (Table 6-4). Fish fed reduced diets, and starved individuals, generally lost energy from tissues.

Energy budgets

Total energy budgets for experiments with maximum rations, 1988-90, accounted for 72-104 % of the energy in balanced budgets ((G+R+F+U)/C · 100) (Table 6-5, Figure 6-7). Growth contributed most to the budget of small fish fed high energy diets of Calanus, whereas respiration contributed most to the budgets of larger fish fed low energy diets of capelin. An average energy

budget (1989 and 1990 budgets combined) for juvenile Arctic cod fed arctic zooplankton (Table 6-5) was:

$100\ C = 50\ G + 33\ R + 3\ F + 6\ U + 8\ Z$

where Z was activity and other unaccounted for energy. Energy budgets for reduced rations and starved individuals were considerably off balance (Table 6-5), except for Parathemisto-fed fish (112 %).

In the 1990 experiment we estimated the maintenance ration (G = 0) to be 716.3 $J \cdot d^{-1}$ (Figure 6-6b). If we use the 1990 values for reduced ration, with F as a fraction of the estimated maintenance ration, we get:

$100\ C = 41\ R + 2F + 7U + 50\ Z$

which implies that active metabolism may account for 50 % or 358 $J \cdot d^{-1}$. If this value is added to the 1990 budget for maximum ration the balance becomes 93.6 %.

Growth and assimilation efficiencies

Gross (GGE) and net (NGE) growth efficiencies varied considerably in experiments (Table 6-5). Mean values for the above combined budget were 50 %, and 60 %, respectively (lower if active metabolism is included). Assimilation efficiencies (AE) were generally lower for capelin than for arctic zooplankton, and higher for group experiments involving capelin than in experiments on individuals (Table 6-5). A mean value for the combined budget was about 80 %, although values in different experiments on maximum rations varied from 64-91 % (Table 6-5).

Discussion

Arctic cod feed primarily on planktonic copepods and amphipods, ice-associated amphipods, and mysids (Bain and Sekerak 1978; Craig et al. 1982; Bradstreet et al. 1986; Lønne and Gulliksen 1989). However, the energy budget for Arctic cod at low temperatures ($100\ C = 50\ G + 33\ R + 3F + 6\ U + 8\ Z$)

differed substantially from a generalized budget for carnivorous fish; 100 C = 29 G + 44 R + 20 F + 7 U (Brett and Groves 1979), and it also differed from the energy budget of an antarctic fish (N. neglecta): 100 C = 6 G + 74 R + 20 (F+U) (Everson 1970). The assimilation efficiency for Arctic cod was about 10 % higher than the generalized budget, but it was similar to the antarctic budget (80 %), probably since assimilation efficiency increases with decreasing temperature (Elliott 1976). However, the gross growth efficiency was much higher for Arctic cod (50 %) than for both the generalized budget (29 %) and the antarctic fish budget (6 %). In particular the antarctic fish allocated a much higher proportion of the energy to respiration, which was attributed by Everson (1970) to metabolic cold adaptation (Wohlschlag 1960), although Holeton (1974) questioned whether this phenomenon was real or a stress-induced artifact.

Even if growth was a main component of the budget for Arctic cod, it was low absolutely, resulting from low daily food intake. Relative growth rates, in our experiments with maximum rations, ranged from 0.6-1.5 % body weight · d^{-1}, depending on fish size. However, the growth rate of wild fish was considerably less, about 0.25 % body weight · d^{-1} between age-1 and 2, and 0.15 % · d^{-1} between age-2 and 3 (from size-at-age relationship; Hop et al., in press). In an enclosure experiment (10 m^3 cage) with age-1 Arctic cod (n=12, mean weight 6.7 g) in Resolute Bay, the mean growth rate during August was 0.45 % body weight · d^{-1} (H. Hop, unpubl. data), which was higher than the annual growth rate, but lower than growth rates for similarly sized fish fed maximum rations in the laboratory (1.0 % body weight · d^{-1}).

Our budgets for fish fed maximum rations accounted for 72-104 % of the energy, which is comparable to other budgets reported in the literature (e.g., Brafield 1985). However, most reported budgets are not complete, some parameters being estimated by difference or proportion. In our energy budgets, consumption and growth were probably determined most accurately. Both

dry/wet weight ratios and energy content of Arctic cod were similar to those reported by Brekke (1989) from Spitsbergen waters.

Our respiration values used were short-term acclimated VO_2 values determined for juvenile Arctic cod (Hop and Graham, in prep.), which were 70-90 % above long-term acclimated (> 5 months) values (Hop and Graham, in prep.). We included feeding metabolism in our values, but not active metabolism. Our estimate of active metabolism, based on maintenance rations in the 1990 experiment, indicated that our respiration values were low, which would partly explain why some of the budgets did not add to 100 %. Even if fish were confined to individual boxes and activity was low, they were disturbed daily during cleaning and feeding, which would elevate respiration rates.

Faecal matter, contained in mucous membranes, were easily collected daily from each compartment, and we probably recovered most of it. We did not account for leakage, and thus our values are underestimates, but leakage may be low at these low temperatures. Excretion values may also have been underestimated, since they were determined for confined animals at rest.

Energy budgets for fish fed reduced rations were considerably unbalanced (except for the 1989 budget with Parathemisto). In these budgets consumption values were low, and small errors in the determination of this or other components would tend to throw the budgets off balance. Budgets for starved individuals also did not balance. In the 1989 experiment weight loss was probably less than it should have been since fish fed on small zooplankton passing through the filtering system. This may also have affected the reduced ration budgets of that year, but probably had little effect on the maximum ration budgets. Weight loss values for the 1990 experiment were probably accurate since the filter system was improved, with no zooplankton passing through.

Our value of daily food intake, measured at maximum rations in the laboratory, is probably higher than food intake of Arctic cod in the wild, which is also affected by food availability and fish behavior. Although dispersed

Arctic cod generally feed, schooling cod had high frequencies of empty stomachs (65 % on average) (Hop et al., in press). Stomach analyses showed that mean stomach fullness of dispersed fish was 32 % of the maximum possible (Hop and Tonn, in prep.), although fish fed to satiation in the 1990 experiment also had similar mean stomach fullness (30 % of maximum) when dissected after the experiment. This may indicate that non-schooling fish may feed near sustained satiation level, on average, even if stomachs are less than maximum full.

Clarke (1983) concluded that low energy intake in polar invertebrates, as compared with temperate ones, may be an adaptation to cold water. In a typical polar marine invertebrate, growth is slow and seasonal, basal metabolism low, annual individual reproductive effort reduced, and the cost of activity about the same when compared with related warmer water species. Since the metabolism is low, the growth efficiency is high, although the growth is slow because of low food intake (Clarke 1983). The energy budget for Arctic cod indicates a similar pattern for arctic fish. Low food intake for wild Arctic cod probably partly results from low food availability. However, low daily rations for fish fed to satiation indicates that slow rates of gastric evacuation may limit food intake when food is abundant. It can take up to two weeks for Arctic cod to evacuate full stomachs (Hop and Tonn, in prep.). Since enzymatic activity is temperature dependent, digestion rates may therefore be limited by low temperatures.

Estimated daily rations of Arctic cod, determined in gastric evacuation experiments (Hop and Tonn, in prep.), resulted in values similar to those of this study. Juveniles (mean weight 6.6 g) fed Calanus and Parathemisto evacuated about 0.22 g · d^{-1} within the first 24 h, and 0.14 g · d^{-1} at half-time (±12 h), the time when half of the stomach content of a full stomach was evacuated. Since fish fed to satiation had less than full stomachs, daily ration values in our study are probably closer to daily rations estimated from half-time evacuation values (Hop and Tonn, in prep.). If, additionally, the daily ration of Hop and Tonn

(in prep.) is adjusted for fish weight (to 5.8 g, the mean weight of fish in the 1989 experiment) based on the relationship between MDR_w and fish weight (Figure 6-5b), the resulting value (0.12 g · d^{-1}) approaches our 1989 estimate of daily rations of arctic zooplankton (0.11 g · d^{-1}). Daily rations, determined from gastric evacuation half-time values for larger fish (0.4-0.5 g · d^{-1}; Hop and Tonn, in prep.) were also similar to our values for large fish (0.5 g · d^{-1}). Jensen et al. (1991) found that daily rations for Arctic cod (10-34 g), fed peeled shrimp (4.31 kJ · g^{-1}) to satiation four times per week, varied from 0.12 and 0.22 g · d^{-1} during periods of low (January - February) and high (September - December) food intake. Their high value is about half of our daily ration value for Arctic cod (26 g) fed capelin, indicating that their fish fed below satiation level.

Arctic cod has been described as an r-selected species (Craig et al. 1982; Mikhail 1985), since it is a small (< 30 cm fork length), relatively short lived (maximum life span of 7 years) fish that reaches maturity at an early age (2-3 years) (Bain and Sekerak 1978; Craig et al. 1982; Bradstreet et al. 1986). Mortality rates are high with relatively few fish surviving past 4 years (Welch et al. 1993, Hop et al., in press). However, some life history aspects, such as slow growth and relatively low fecundity (Andiyashev 1954; Hop et al., in prep.), do not fit an r-selected pattern (Adams 1980).

Growth of Arctic cod is not directly comparable to other gadids since none of the other species live continuously at similarly low ambient temperatures. The growth rate of Arctic cod in the Canadian High Arctic (Hop et al., in press) is much slower than that of Greenland cod (Gadus ogac Richardson, 1836) in Hudson Bay (Mikhail and Welch 1989), a species that has been described as K-selected with slow growth (Mikhail 1985). The geographic range of Greenland cod overlap partially with Arctic cod in northern Labrador and Greenland, and but the growth rate of Arctic cod off the coast of Labrador (Lear 1983) remained below that of slow growing Greenland cod in Hudson Bay (Mikhail and Welch 1989). However, the growth rate of Arctic cod was higher

than that of sympatric benthic species, such as snailfishes (Falk-Petersen et al. 1988).

Arctic cod had high growth- and assimilation efficiencies at low temperatures, which means that they are efficient converters of zooplankton to fish flesh. However, the growth of individual fish was slow since low metabolic energy costs was partly balanced against low food intake. Given slow growth, a large annual production of Arctic cod must be a result of a high growth efficiency coupled with high standing biomass.

Arctic cod are the dominant prey of several seabird and marine mammal species in the Canadian High Arctic (Bradstreet et al. 1986; Welch et al. 1992, 1993). The annual predation on Arctic cod by seabirds and marine mammals in the Lancaster Sound Region, was estimated to be in the order of 148,000 metric tons (Welch et al. 1992). This estimate was about 25 times higher than the abundance estimate for dispersed cod (0.962 $g \cdot m^{-2}$), or 6,000 tons for the entire region (Welch et al. 1992). The estimate of the standing stock is probably much too low, probably because aggregated or schooling cod were not properly accounted for. Schooling may be a widely distributed phenomenon in time and space (Ponomarenko 1967, 1967; Rass 1968; Bain and Sekerak 1978; Andriyashev et al. 1980; Craig et al. 1982), but it is mainly observed during the open water season in the Canadian High Arctic (Welch et al. 1993). Presumably a large fraction of the Arctic cod biomass is concentrated in schools at volume densities up to 10 $kg \cdot m^{-3}$ (Crawford and Jorgenson, in press). Even though some estimates of Arctic cod abundance have been conducted by hydroacoustic surveys in open water (Crawford and Jorgenson 1993; Crawford and Jorgenson, in press.) and beneath the ice on landfast ice edges (Crawford and Jorgenson 1990), no large-scale estimates exist for the standing stock of Arctic cod in the Canadian High Arctic. The annual production of Arctic cod must at least equal the annual predation (148, 000 tons). If one assumes that the mean annual growth rate of the standing biomass of Arctic cod is about 0.5 (based on a mean growth rate of 0.15 $\% \cdot d^{-1}$ of fish between age-2 and 3) the standing

biomass must be at least 300,000 tons in the Lancaster Sound Region, or five times the existing biomass estimate.

Since the key position of Arctic cod in the high arctic marine food web is linked to their high standing biomass, any reduction of this biomass could have detrimental effects on higher trophic levels, marine mammals and seabirds, similar to what has been recorded elsewhere. The collapse of Atlanto-Scandian herring (Clupea harengus L.) stocks in the late sixties reduced Atlantic puffin (Fratercula arctica) populations substantially (by 60 % in some areas), and the collapse of Barents Sea capelin (M. villosus) stocks in 1985-86 caused moderate (30-40 %) to severe (80-90 %) reductions in Thick-billed murre (Uria lomvia) and Common murre (U. aalge) colonies, respectively (Vader et al. 1989; Vader et al. 1990). In both cases the energy flow through the food chain was changed, and the changes involved key components at an intermediate trophic level. To understand and model changes in energy flow through food webs, one first has to know the energy budgets of individual components in unaltered systems, particularly the important ones such as Arctic cod in the high arctic food web.

Table 6-1. Absolute and relative growth rates, daily rations and faecal matter of Arctic cod fed different diets; capelin fillets, Calanus copepods, and Parathemisto amphipods. Maximum (satiation) and reduced (close to maintenance) rations were fed to individuals, or groups of marked fish. Data are means ± SE for individual fish (n), with weights as wet weight except for faeces (dry weight).

Experiment (year)	Diet	n	Duration (d)	Fish weight (g)	Growth rate ($mg \cdot d^{-1}$)	Growth rate ($\% \cdot d^{-1}$)	Daily ration ($no. \cdot d^{-1}$)	Daily ration ($mg \cdot d^{-1}$)	Daily faeces ($mg \cdot d^{-1}$)
Maximum ration									
1988	Capelin	3	56	3.99±1.99	53.2±21.3	1.487±0.162	-	130.1±66.8	0.739±0.169
1988	Capelin	4	56	26.29±2.32	150.4±18.1	0.577±0.057	-	408.5±27.6	1.454±0.227
1988	Capelin	7	56	59.18±4.01	146.6±19.1	0.253±0.032	-	647.7±65.7	2.139±0.182
1988	Capelin [a]	12	56	40.28±2.32	177.0±16.1	0.449±0.042	-	470.3	2.006
1988	Capelin [a]	12	28	41.90±2.30	241.2±20.0	0.588±0.046	-	560.8	1.151
1989	Calanus	5	48	4.93±0.63	56.3±5.7	1.179±0.105	10.15±1.26	98.5±12.2	1.174±0.090
1989	Parathemisto	5	48	4.40±0.40	38.0±3.9	0.908±0.142	5.51±0.18	112.9±3.7	5.130±1.564
1990	Calanus	8	36	11.21±0.46	62.6±8.8	0.551±0.064	17.93±1.65	168.0±14.8	2.772±0.666
Reduced ration									
1989	Calanus [b]	5	24	5.08±0.51	12.9±1.9	0.254±0.033	2.15±0.21	20.9±2.0	0.463±0.077
1989	Calanus [c]	5	24	5.39±0.54	- 0.4±1.8	0.003±0.027	1.10±0.10	10.7±1.0	0.463±0.054
1989	Parathemisto [b]	5	24	4.14±0.63	8.2±1.9	0.221±0.063	2.14±0.20	43.6±4.1	0.994±0.120
1989	Parathemisto [c]	5	24	4.33±0.62	19.1±6.0	0.412±0.064	1.20±0.20	24.6±4.1	1.504±0.248
1990	Calanus	10	36	11.66±0.34	- 10.9±5.2	- 0.089±0.044	3.02±0.02	28.4±1.6	0.666±0.046
Starvation									
1988	none	12	20	47.46±2.47	- 80.8±17.5	- 0.173±0.033	0	0	0.386
1989	none	8	48	5.19±0.22	- 7.1±1.0	- 0.134±0.018	0	0	0
1990	none	10	36	11.99±0.41	- 42.9±3.8	- 0.357±0.028	0	0	0

[a] group experiment
[b] two prey items daily
[c] one prey item daily

Table 6-2. Dry/wet weight, energy, lipid, and protein contents in samples (n) of prey and Arctic cod. Values for juveniles included whole fish, whereas values for adults were calculated based on wet weight contributions and respective energy, lipid and protein contents of four tissues (carcass, liver, intestine, and gonad). Fish samples were frozen (prior to dissection), and stomach contents were excluded. Data are means ± SE.

Source	n	Dry/wet weight	Energy content		Lipids		Protein	
		(%)	(kJ · g^{-1} dry wt.)	(kJ · g^{-1} wet wt.)	(% dry wt.)	(% wet wt.)	(% dry wt.)	(% wet wt.)
Prey								
Capelin	7	20.65±0.35	24.404±0.278	5.039±0.057	16.90±2.05	3.28±0.40	71.46±2.01	13.86±0.39
Calanus	5	31.29±1.48	31.008±0.451	9.702±0.141	50.41±1.26	16.82±0.42	31.03±0.89	10.35±0.30
Parathemisto	6	19.42±1.99	21.086±1.225	4.095±0.238	25.72±1.62	5.61±0.35	39.55±1.21	8.63±0.26
Arctic cod								
Juveniles	15	21.76±0.31	25.539±0.187	5.557±0.041	23.94±0.76	5.39±0.17	55.32±1.11	12.47±0.25
Adults	100	24.71±0.15	26.140±0.092	6.459±0.023	33.53±0.42	8.29±0.10	44.93±0.35	11.10±0.09
Males	50	24.54±0.22	26.138±0.135	6.414±0.033	34.36±0.59	8.43±0.14	44.31±0.47	10.87±0.12
Females	50	24.89±0.20	26.141±0.126	6.506±0.031	32.70±0.59	8.14±0.15	45.55±0.51	11.34±0.13
Male tissues								
Carcass	7	19.68±0.24	21.504±0.331	4.232±0.065	14.25±0.83	2.80±0.16	62.4±0.54	12.28±0.11
Liver	7	73.14±3.04	37.011±0.259	27.070±0.189	83.82±1.54	63.00±1.16	5.33±0.73	4.00±0.55
Intestine	7	27.52±0.71	26.721±0.458	7.354±0.126	23.43±2.73	6.42±0.75	36.23±1.63	9.93±0.45
Gonad	7	32.32±1.16	30.414±0.437	9.830±0.141	48.91±5.38	14.59±1.60	35.71±4.37	10.66±1.30
Female tissues								
Carcass	7	20.05±0.44	22.037±0.276	4.418±0.055	12.87±0.83	2.56±0.16	64.37±0.87	12.80±0.17
Liver	7	68.92±3.94	35.840±0.443	24.701±0.305	79.70±1.95	61.42±1.51	5.63±0.97	4.33±0.74
Intestine	7	29.07±1.14	27.057±0.565	7.865±0.164	28.05±2.45	7.69±0.67	34.85±1.96	9.55±0.54
Gonad	7	28.09±1.08	28.580±0.850	8.028±0.239	44.93±4.38	13.54±1.32	38.74±3.28	11.67±0.99

Table 6-3. Energy content of faecal matter samples (n) collected from fish in the 1988-90 experiments, and from groups of juvenile and adult fish fed specific diets for about four weeks prior to sampling. Faecal matter from wild fish (diets unknown) were sampled within two days of capture.

Experiment (year)	Diet	n	Energy cont. ($kJ \cdot g^{-1}$ dry wt.)
Maximum ration			
1988	Capelin	2	25.214
1989	Calanus	1	11.443
1990	Calanus	1	16.670
Reduced ration			
1990	Calanus	1	9.090
Group collections			
Juveniles (1989)	Calanus	1	11.633
Adults (1989)	Calanus	1	7.446
Juveniles (1989)	Parathemisto	1	4.649
Adults (1989)	Parathemisto	1	4.761
Juv./Ad. (1989)	Unknown	1	8.507
Juveniles (1991)	Unknown	2	6.910

Table 6-4. Dry/wet weight and energy content of fish (n) at the end of feeding experiments. Energy content of individuals in the 1988 experiment was calculated, based on wet weight contributions and respective energy contents of four tissues (carcass, liver, intestine, and gonads). Change in energy content of experimental fish (relative to fish in Table 6-2) is indicated; in the 1988 experiments half of the energy loss was assumed to have occurred before experiments started (1.5 months from time of capture). Fish samples were frozen (prior to dissection), and stomach contents were excluded. Data are means ± SE.

Experiment (year)	Diet	n	Duration (d)	Initial fish weight (g)	Final fish weight (g)	Dry/wet weight (%)	Energy content ($kJ \cdot g^{-1}$ dry wt.)	Energy content ($kJ \cdot g^{-1}$ wet wt.)	± Energy content ($kJ \cdot g^{-1}$ wet wt.)
Maximum ration									
1988	Capelin	3	56	3.99±1.99	6.97±3.18	20.66±0.54	23.180±0.334	4.655±0.189	-0.451
1988	Capelin	4	56	26.29±2.32	34.72±3.00	23.12±0.33	24.059±0.033	5.563±0.086	-0.448
1988	Capelin	7	56	59.18±4.01	67.39±4.38	22.70±0.65	24.035±0.112	5.460±0.175	0.523
1988	Capelin [a]	12	56	40.28±2.32	50.19±2.77	23.27±0.16	24.133±0.082	5.615±0.051	-0.427
1988	Capelin [b]	12	56	41.90±2.30	45.84±2.50	23.12±0.19	24.006±0.097	5.550±0.058	-0.456
1989	Calanus	5	48	4.93±0.63	7.63±0.84	27.37±0.54	27.841±0.100	7.618±0.149	2.061
1989	Parathemisto	5	48	4.40±0.40	6.22±0.31	22.21±0.57	24.717±0.505	5.501±0.250	-0.056
1990	Calanus	8	36	11.21±0.46	13.46±0.70	23.70±0.52	26.415±0.244	6.269±0.195	0.712
Reduced ration									
1989	Calanus	5	48	5.08±0.51	5.38±0.50	22.86±0.45	25.135±0.255	5.750±0.160	0.193
1989	Parathamisto	5	48	4.14±0.63	4.79±0.76	20.34±0.54	23.238±0.457	4.735±0.216	-0.822
1990	Calanus	10	36	11.66±0.34	11.27±0.31	20.25±0.42	23.852±0.328	4.842±0.167	-0.715
Starvation									
1989	none	8	48	5.19±0.22	4.85±0.20	21.63±0.50	24.459±0.357	5.301±0.197	-0.256
1990	none	10	36	11.99±0.41	10.44±0.37	18.84±0.69	22.985±0.436	4.358±0.240	-1.199

[a] group fed to satiation during the whole period
[b] group fed to satiation during the first half of the period and subsequently starved

Table 6-5. Mean daily energy budget ($J \cdot d^{-1}$) in controlled feeding experiments on Arctic cod, 1988-90. Fish weight is mean of initial and final weight (Table 6-4). Consumption (C) is calculated from daily ration and energy content of feed (Tables 6-1, 6-2). Growth (G) is calculated from weight increase and change in energy content of experimental fish (Table 6-4). Respiration (R) is calculated from values of starved and fed fish, adjusted for temperature and fish size (Hop and Graham, in prep.) Egestion (F) is calculated from daily faeces and their energy contents (Tables 6-1, 6-3). Excretion (U) was determined separately as 13.58 and 4.90 μg ammonium $\cdot g^{-1} \cdot h^{-1}$ for fed and starved fish, respectively (we used an intermediate value of 9.24 for reduced rations). Coefficients for conversion of oxygen consumption and ammonia to energy equivalents were used (see Methods). Balance is (G+R+F+U)/C * 100. Gross (GGE) and net (NGE) growth efficiencies, and assimilation efficiency (AE) are indicated (see Methods).

Experiment (year)	Diet	n	Duration (d)	Fish weight (g)	Consumption ($J \cdot d^{-1}$)	Growth ($J \cdot d^{-1}$)	Respiration ($J \cdot d^{-1}$)	Faeces ($J \cdot d^{-1}$)	Excretion ($J \cdot d^{-1}$)	Balance (%)	GGE (%)	NGE (%)	AE (%)
Maximum ration													
1988	Capelin	3	56	5.48	655.6	215.6	226.2	18.6	36.6	75.8	32.88	48.80	67.39
1988	Capelin	4	56	30.51	2058.4	627.1	940.8	36.7	203.8	87.9	30.47	40.00	76.17
1988	Capelin	7	56	63.29	3263.8	247.8	1724.1	53.9	422.8	75.0	7.59	12.57	60.42
1988	Capelin [a]	12	56	45.24	2369.8	686.5	1304.7	50.6	302.2	98.9	28.97	34.48	84.02
1988	Capelin [b]	12	56	46.26	1412.9	49.3	1191.0	19.4	208.2	103.9	3.49	3.97	87.78
1989	Calanus	5	48	6.28	955.6	640.2	256.2	13.4	42.0	99.6	66.99	71.42	93.80
1989	Parathemisto	5	48	5.31	462.3	203.4	218.0	23.8	35.5	104.0	44.00	48.27	91.16
1990	Calanus	8	36	12.34	1629.9	613.5	426.1	46.2	82.4	71.7	37.64	59.01	63.78
Reduced ration													
1989	Calanus	5	48	5.23	153.3	56.4	157.6	4.2	23.8	157.8	-	-	-
1989	Parathemisto	5	48	4.47	140.0	-6.8	137.3	5.8	20.3	111.8	-	-	-
1990	Calanus	10	36	11.47	275.5	-284.0	291.9	6.1	52.1	24.0	-	-	-
Starvation													
1989	none	8	48	5.02	0	-65.2	153.7	0	12.1	39.3	-	-	-
1990	none	10	36	11.22	0	-587.0	289.1	0	27.0	185.7	-	-	-

[a] group fed to satiation during the whole period
[b] group fed to satiation during the first half of the period and subsequently starved

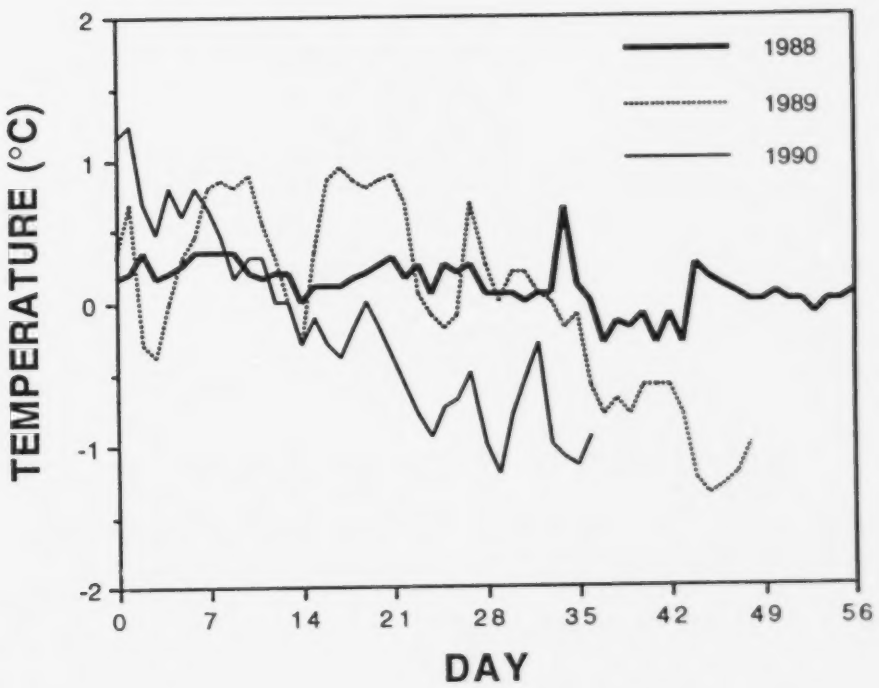

Figure 6-1. Daily temperatures in feeding experiments, 1988,-89,-90.

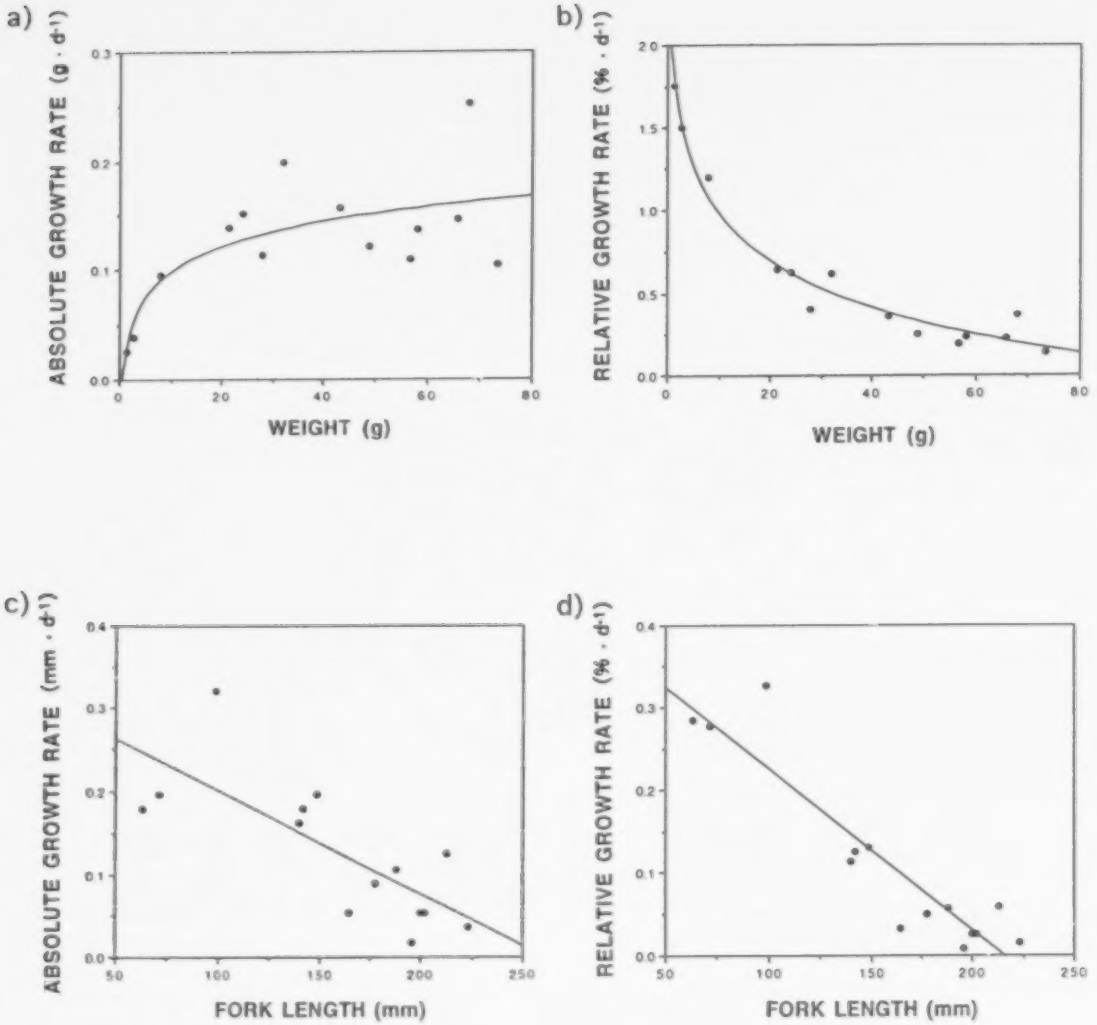

Figure 6-2. Growth rates of Arctic cod (W_1 = initial weight; L_1 = initial length) fed satiation diets of capelin, in 1988 experiments.

a) Absolute growth rate ($g \cdot d^{-1}$) fitted by logarithmic regression:

$G_1 = 0.02068 + 0.03336 \ln (W_1)$, $r^2 = 0.512$.

b) Relative growth rate ($\% \cdot d^{-1}$) fitted by logarithmic regression:

$G_2 = G_1/W_1 \cdot 100 = 1.9248 - 0.4101 \ln (W_1)$, $r^2 = 0.971$.

c) Absolute growth rate ($mm \cdot d^{-1}$) fitted by linear regression:

$G_1 = 0.32415 - 0.00124 L_1$, $r^2 = 0.598$.

d) Relative growth rate ($\% \cdot d^{-1}$) fitted by linear regression:

$G_2 = G_1/L_1 \cdot 100 = 0.42114 - 0.00196 L_1$, $r^2 = 0.865$.

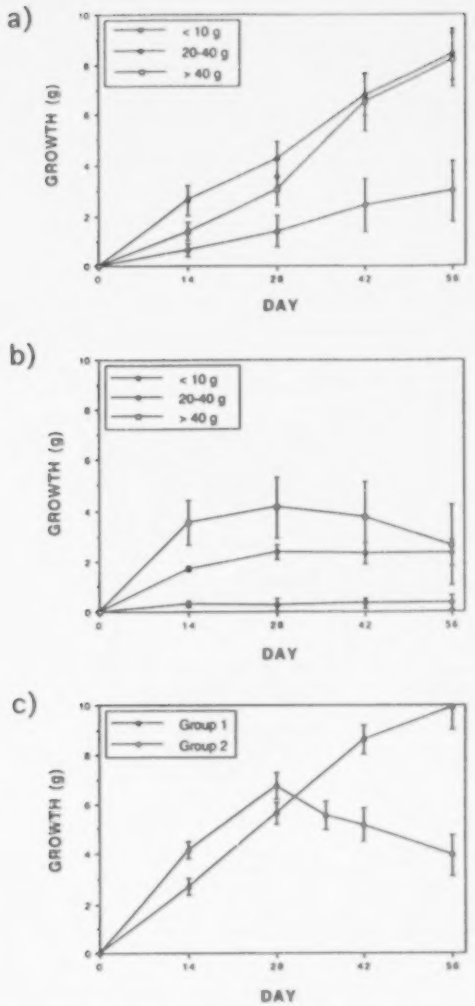

Figure 6-3. Absolute growth (change in wet weight) of Arctic cod in feeding experiments on individuals (a, b) and groups (c), 1988. Fish were fed chopped capelin fillets. Means (± SE) for growth of individual fish are indicated.

a) Maximum (daily feeding to satiation) rations for different size- groups: < 10 g (n=3); 20-40 g (n=4); > 40 g (n=7).

b) Reduced ration, a percent body weight ration which declined by half every two weeks (2, 1, 0.5, 0.25 %), fed different size-groups: < 10 g (n=2); 20-40 g (n=6); < 40 g (n=4).

c) Two groups of fish (n=12) fed maximum rations during the first 28 days. During the next 28 days maximum rations were continued for group 1, while group 2 was starved. The two groups (1, 2) had similar mean (± SE) weight at the start of the experiment (40.28 ± 2.32 g, 41.90 ± 2.30 g).

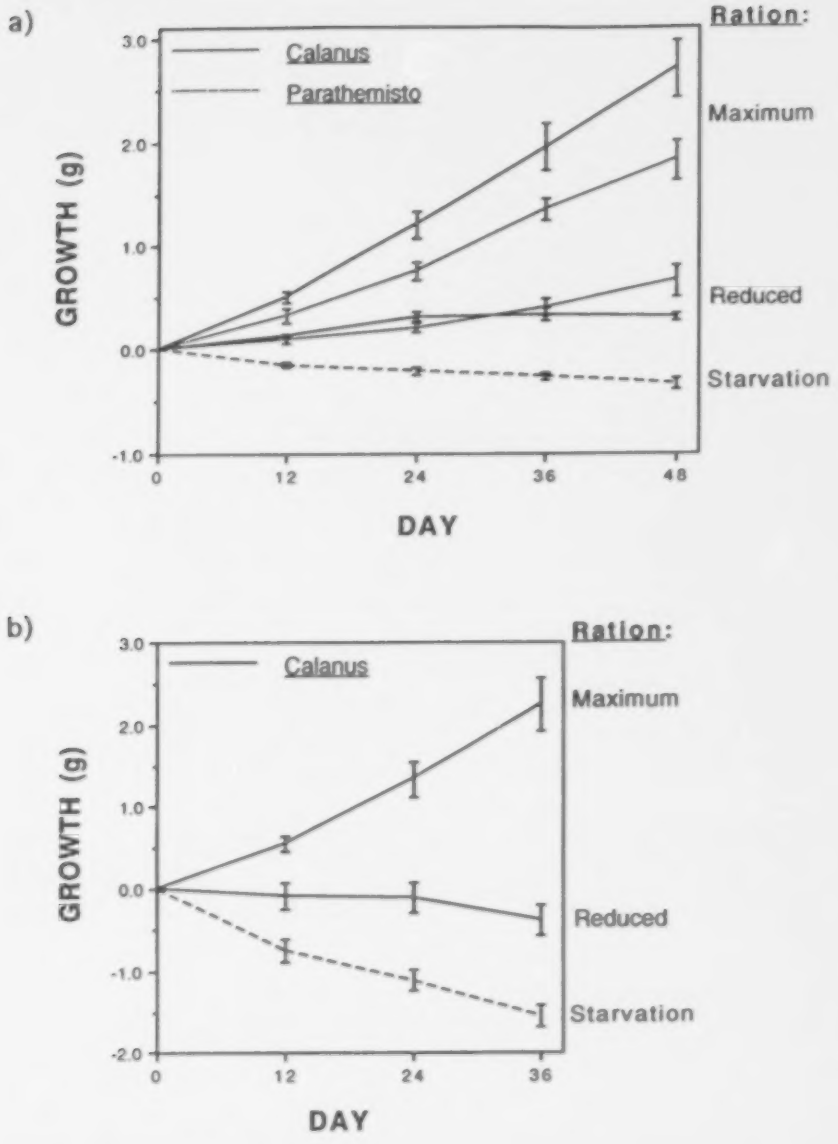

Figure 6-4. Absolute growth (change in wet weight, mean ± SE) of Arctic cod in feeding experiments on individuals with three different rations: maximum (daily feeding to satiation), reduced (adjusted close to maintenance), and starvation.

a) 1989 experiment, fish fed Calanus and Parathemisto: maximum rations (n=5 each), reduced rations (n=5 each), and starvation (n=8).

b) 1990 experiment, fish fed Calanus: maximum ration (n=8), reduced ration (n=10), and starvation (n=10).

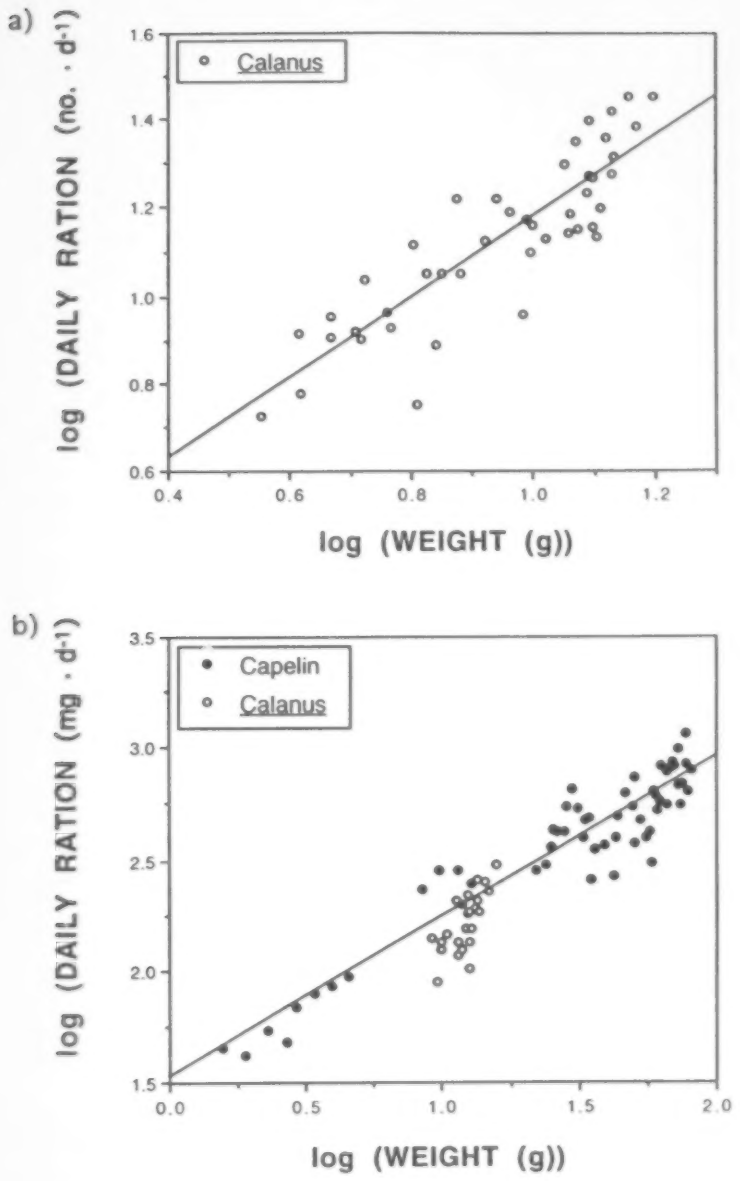

Figure 6-5. Maximum daily rations (MDR) presented as (a) numbers (MDR_n) or (b) weight (MDR_w) of Calanus copepods and capelin fillets, consumed over 12-14 day periods, as a function of wet weight (W) of Arctic cod.

a) $\log (MDR_n) = 0.9191 \log (W) + 0.2608$, $r^2 = 0.761$.

b) $\log (MDR_w) = 0.7138 \log (W) + 1.5272$, $r^2 = 0.896$.

MDR_w of Calanus is plotted for comparison, but not included in the regression.

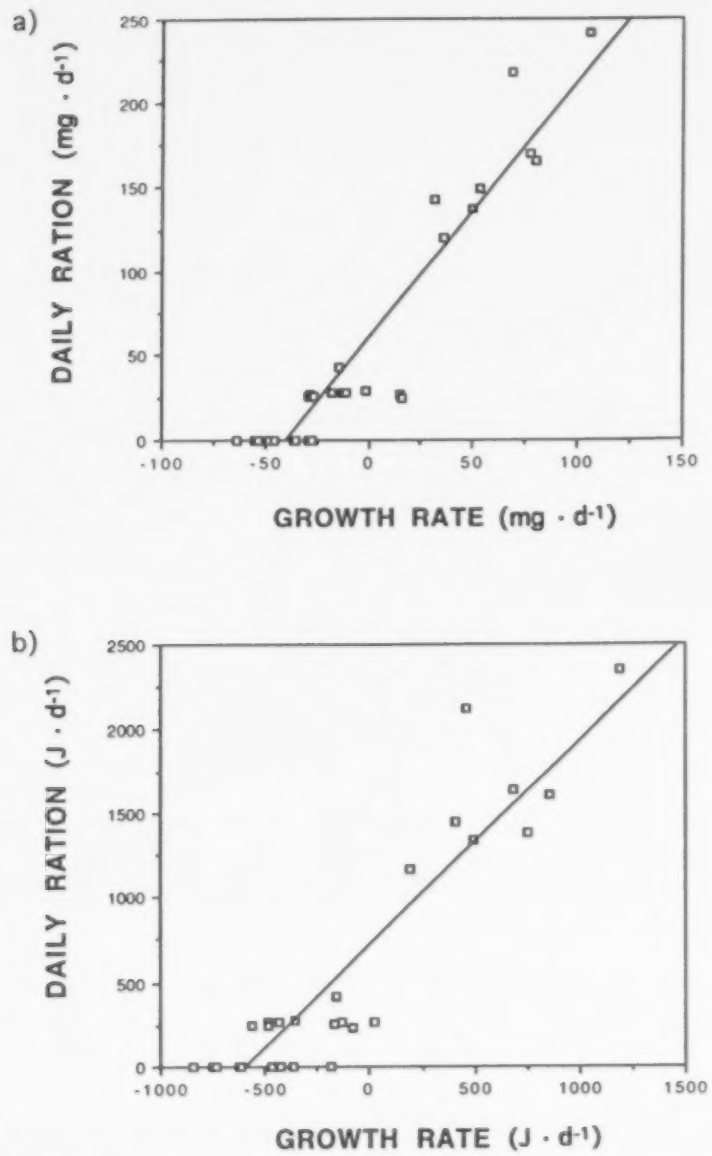

Figure 6-6. Mean daily ration (DR) against growth rate (G_1) for Arctic cod, in feeding experiment 1990.

a) Weight of daily ration (DR_w) regressed against growth rate:

$DR_w = 60.163 + 1.5120\ G_1$, $r^2 = 0.890$.

b) Energy of daily ration (DR_e) regressed against growth rate, including change in energy content of experimental fish:

$DR_e = 716.32 + 1.2117\ G_1$, $r^2 = 0.851$.

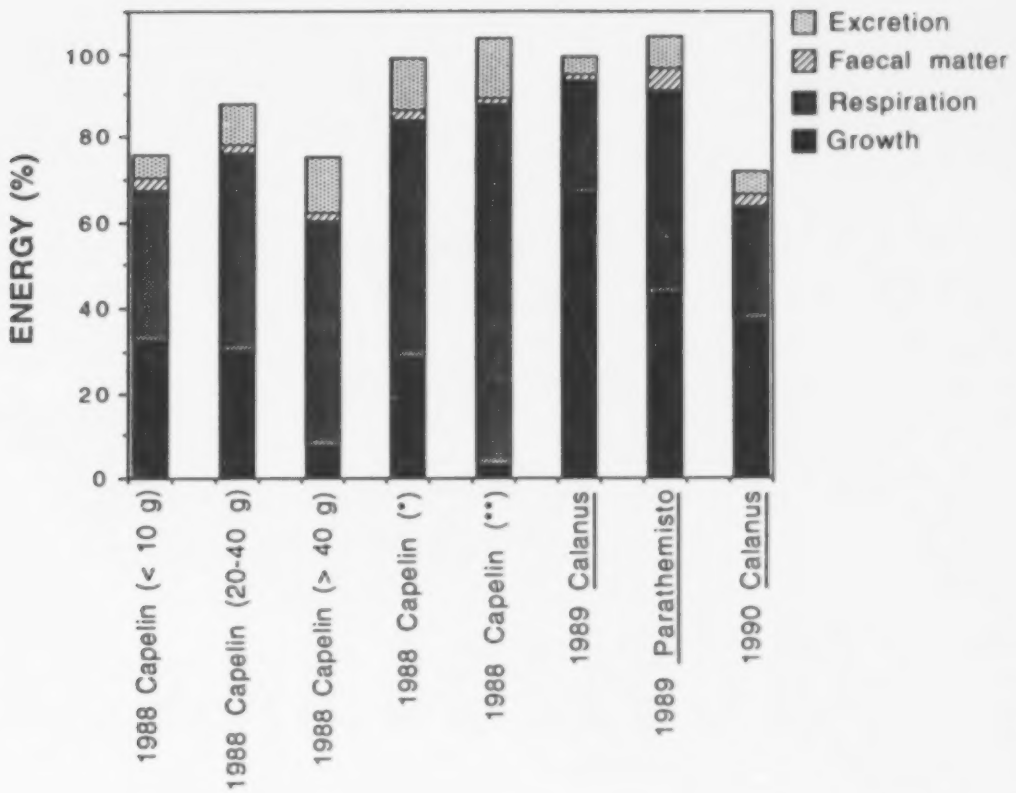

Figure 6-7. Energy budgets for experimental groups fed maximum rations. 1988-experiments included capelin diets fed to three size-classes of individual fish (< 10, 20-40, > 40 g) and two groups of fish (* fed to satiation during the whole period, ** fed to satiation during the first half of the period and subsequently starved). 1989 and 1990 experiments included individuals fed Calanus or Parathemisto. Components of energy budgets are expressed as % of total energy ingested (a fully balanced budget adds to 100 %).

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CHAPTER 7

General conclusions

General conclusions

The feeding ecology and bioenergetics of Arctic cod differed from those of more temperate gadids such as Atlantic cod (Gadus morhua L.) and Pacific cod (G. macrocephalus Tilesius, 1810) (e.g., Jones and Hislop 1978; Jobling 1982, 1988; Paul et al. 1990). The Greenland cod (G. ogac Richardson, 1836), which overlaps in distribution with Arctic cod on the coasts of Northern Labrador, Newfoundland and western Greenland (Scott and Scott 1988), was more similar to the other gadids than to Arctic cod. Arctic cod feed pelagically, whereas the other gadids are predominately benthic feeders (Brawn 1969; Jewett 1978; Mikhail 1985; Mikhail and Welch 1989). The other species also have faster growth rates, greater consumption rates, and grow to a larger maximum size. The feeding ecology, behavior, age of first maturity, and maximum size of Arctic cod are thus more similar to capelin (M. villosus Müller, 1777) (Scott and Scott 1988). Both species school in large aggregations seasonally and are key components of marine food webs (Vader et al. 1989, 1990; Welch et al. 1992), although Arctic cod prefer colder temperatures than capelin (Hognestad 1968; Falk-Petersen et al. 1986) and have different reproductive behavior and spawning time. Whereas capelin spawn in shallow water or on beaches during the summer (Jangaard 1970), Arctic cod spawn during the winter under the ice (Andriyashev 1954; Rass 1968).

Arctic cod have been observed in large aggregations or schools in Canadian high arctic waters (Bain and Sekerak 1978; Welch et al. 1993). Two types of schools were observed on the coasts of Cornwallis and Devon Islands; juvenile schools occurring in July in association with broken ice over relatively shallow water, and schools of adults occurring later (August - September) during the open water season. Juvenile schools seemed to be feeding aggregations, whereas adults in schools only fed occasionally and generally had high frequencies of empty stomachs. In addition, dispersed

individuals were present throughout the season, and these fish were generally feeding. Adult Arctic cod therefore exhibited two behavioral strategies: they either participate in schools with reduced feeding intensity, or disperse to feed as individuals. Since schools may persist in one area for up to two months (Welch et al. 1993), one would predict that fish would lose weight if they were not feeding, and thus have lower condition factor. However, since the weight loss of Arctic cod is slow at low ambient temperatures, there was no significant difference between condition factors of schooling and non-schooling individuals, although the mean condition factor was slightly lower for schooling fish.

Low estimated weight loss (< 10 % · month^{-1}) was due to low respiration rates at ambient low temperatures. Respiration rates, measured for short-term acclimated Arctic cod in the laboratory, may be similar to that of fish in the wild, assuming that the decrease in VO_2 due to long-term acclimation approximately equals the increase in VO_2 because of increased activity. However, the finding that long-term acclimation (5 months) reduced VO_2 to about half of the short-term VO_2 values, supported Holeton's (1974) view that the phenomenon of metabolic cold adaptation (Scholander et al. 1953; Wohlschlag 1960) was mainly a stress-induced artifact because of short-term acclimation to laboratory conditions. Feeding also increased oxygen consumption (specific dynamic action) 23-62 % above pre-fed levels, depending on fish size, rations and acclimation time. Due to slow evacuation rates, SDA for Arctic cod in the wild will probably remain elevated during periods of feeding. Respiration rates of Arctic cod were similar to those reported for other gadids (e.g., Greenland cod, Pacific cod) when both fish-size and temperature in the other studies (Mikhail 1985; Paul et al. 1988) were adjusted for direct comparisons. Therefore, the Arctic cod appears not to have special metabolic adaptations for living at low temperatures.

One adaptation, that makes it possible for Arctic cod to live in cold water, is the presence of glycoprotein in the blood which causes freezing point

depression (Osuga and Feeney 1978). These macromolecules thus function as antifreeze and prevents tissues from freezing at sub-zero temperatures when fish come in contact with ice (Van Voorhies et al. 1978). This adaptation coupled with morphology, such as oblique superior mouth and slender, streamlined body, has then allowed for exploitation of the abundant epontic (cryopelagic) or ice-associated communities of invertebrates (Andriyashev 1970; Gulliksen and Lønne 1989; Lønne and Gulliksen 1989). Other morphological characteristics such as long pelvic fin rays, large eyes and dusky color are rather adaptations to reduced light conditions in the arctic. Benthic fish species in the Arctic (i.e., zoarcids and cottids) have no antifreeze adaptation; they are supercooled and will freeze when brought in contact with ice (Scholander et al. 1957). However, Arctic cod are also relatively tolerant of fluctuations in both temperature and salinity (Craig et al. 1982), and the question remains as to why Arctic cod are not distributed further south. The Arctic cod is almost the sole occupant of the pelagic fish niche in circumpolar arctic waters, besides the sparsely distributed polar cod (Arctogadus glacialis Peters, 1874) and toothed cod (A. borisovi Drjagin, 1932) (Nielsen and Jensen 1967; Boulva 1972, 1979). The lack of competitors, that are adapted to live at sub-zero temperatures, has likely contributed to the success of Arctic cod in this environment. Potential competition with capelin, herring and other species for the same pelagic food resources may limit its southward distribution. Larger predatory fishes, such as the large gadid species, are also conspicuously absent from high arctic waters. The Greenland shark (Somniosus microcephalus Bloch and Schneider, 1801) prey on arctic fish, but this species has a limited distribution and is mainly restricted to deep waters (Templeman 1963). Instead marine mammals, particularly ringed seals, harp seals, and beluga whales, fill the piscivorous niche and often prey heavily on both schooling fish and dispersed individuals (Bradstreet et al. 1986; Finley et al. 1990; Welch et al. 1993).

The Arctic cod functions as a key species in the high arctic food web since it is the main prey for several species at higher trophic levels. Ecological equivalents are capelin in the Barents Sea and northwest Atlantic, herring (Clupea harengus L.) and sand lances (Ammodytes spp.) in the North Sea, walleye pollock (Theragra chalcogramma Pallas, 1811) in the Bering Sea, and Northern anchovy (Engraulis mordax mordax Girard, 1854) on the coast of California. A large portion of the energy flow in the respective food webs is channeled through these key components, but to estimate this energy flow one first has to establish energy budgets for individual components. A main point of this thesis was to establish an energy budget for Arctic cod.

The energy budget of Arctic cod indicated that growth was high relative to respiration and waste losses, although the absolute growth was low because of low food intake. This budget differed from the generalized budget of carnivorous fish (Brett and Groves 1979) and that of an antarctic fish (Everson 1970). Although assimilation efficiency was similar to the antarctic budget (about 80 %), the gross growth efficiency of Arctic cod was much higher, since less energy was allocated to respiration. The growth efficiency of wild Arctic cod may be slightly lower because of activity, but the effect of active metabolism may be counteracted by long-term acclimation, which would lower metabolism as previously mentioned.

Even if metabolic costs were low, low daily food intake at ambient temperatures resulted in slow growth rates for different size-classes of Arctic cod. Daily consumption rates were affected by slow gastric evacuation rates, due to slow digestive processes at low temperatures. Evacuation rates were not higher than what would be expected by extrapolating from gastric evacuation rates determined for other species at higher temperatures (Elliott 1972; Persson 1979), indicating that Arctic cod do not have special cold-adapted digestive enzymes. Probably all body functions for this fish are just slower at low temperatures.

One additional energy allocation, which was not dealt with in the energy budget, was investment in reproduction. Potential energy loss during spawning was determined separately for ripe Arctic cod that had been sustained in the laboratory until the time of spawning (mid February). Ripe females contained few eggs relative to other gadids and the eggs were large. However, the gonadosomatic index and energy invested in gonad production were greater for Arctic cod than for other gadids (Eliassen and Vahl 1982; Smith et al. 1988, 1990). Most gadids, including Arctic cod, have large livers where energy is stored as triglycerides. Energy is then drawn from this source, and from somatic tissue, during gonad production (e.g., Kjesbu et al. 1991). Despite investing large amounts of energy in reproduction, no mortality resulted from spawning under laboratory conditions, and it appeared that Arctic cod may be repeat spawners (Graham and Hop, in prep.). However, post-spawning morality in nature may be high since few fish live past age-4 (Nikol'skii 1954; Moskalenko 1964), which implies that fish in the wild may typically spawn only two times. Early maturation and high energy output during spawning may be balanced against high predation rates on this species during the open water season (Welch et al. 1992; Welch et al. 1993). Repeated spawning for this species would likely enhance fitness, since the total reproductive output for an individual would be higher if the fish can spawn twice and spawn at a larger size when the fecundity is greater. However, the chance of an individual surviving to the next spawning season may be rather low because of predation and natural mortality. A high energy investment in the first reproduction must be a successful strategy for Arctic cod, given the high abundance of this species in the Canadian High Arctic.

Predation on Arctic cod by seabirds and marine mammals in the Lancaster Sound Region, was estimated to be in the order of 148,000 metric tons annually (Welch et al. 1992). This estimate was about 25 times higher than the abundance estimate for dispersed cod (0.962 $g \cdot m^{-2}$), or 6,000 tons for the entire region (Welch et al. 1992). The estimate of the standing stock is

probably much too low, probably because aggregated or schooling cod were not properly accounted for. Schooling may be a widely distributed phenomenon in time and space (Ponomarenko 1967, 1967; Rass 1968; Bain and Sekerak 1978; Andriyashev et al. 1980; Craig et al. 1982), but it is mainly observed during the open water season in the Canadian High Arctic (Welch et al. 1993). Since the growth of individual fish was slow, a high annual production must result from a large standing biomass of fish. Even though some estimates of Arctic cod abundance have been conducted by hydroacoustic surveys in open water (Crawford and Jorgenson 1993; Crawford and Jorgenson, in press.) and beneath the ice on landfast ice edges (Crawford and Jorgenson 1990), no large-scale estimates exist for the standing stock of Arctic cod in the Canadian High Arctic. The standing stock in the Lancaster Sound Region is probably at least twice that of the total annual predation on Arctic cod, i.e., > 300,000 metric tons. Future research should therefore focus on broader scale estimates of Arctic cod biomass, such as the ones conducted in the Barents Sea (Monstad and Gjøsæter 1987), although the short open-water season in the Canadian High Arctic represents a problem for extensive hydroacoustic estimates of this species.

Production by the second trophic level (zooplankton) also appeared insufficient to satisfy the annual consumption by higher trophic levels (Welch et al. 1992). This may be partly because estimates of zooplankton production were too low and because growth efficiencies between trophic levels were underestimated. It was evident from controlled feeding experiments that net growth efficiency of Arctic cod may be much higher (60 %) than that initially reported (35 %; Welch et al. 1992). This would imply that less zooplankton biomass is needed to sustain the annual production of Arctic cod than was previously estimated. High growth and assimilation efficiencies at low and intermediate trophic levels may explain why high arctic food chains can be long (five trophic levels; Hobson and Welch 1992). There is therefore a need to re-examine production efficiencies of other parts of the arctic food web, since

these also may be high at low temperatures. Better quantiative information of food consumption of Arctic cod in the field is also needed, included estimates of the contribution of various prey groups to the overall diet. Finally, little information exists for Arctic cod and the lower trophic levels (zooplankton and benthos) during the winter season in high arctic waters, although an ongoing full-year study by H.E. Welch (Department of Fisheries and Oceans, Canada) and associates may resolve some of these gaps in our knowledge about the high arctic food web.

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APPENDIX 1

Energy of stomach contents from seabirds
in the Canadian High Arctic

An expanded version of this appendix will be submitted for publication, as a manuscript co-authored with Keith A. Hobson.

Introduction

Many seabird species in the Canadian High Arctic depend on Arctic cod (Boreogadus saida Lepechin, 1774) as a key element of their diets, in addition to several pelagic and ice-associated invertebrates (Bradstreet 1980; Gaston and Nettleship 1981; Bradstreet and Cross 1982; Bradstreet et al. 1986; Welch et al. 1992). Seabirds that prey on Arctic cod in the vicinity of Cornwallis and Devon Islands, N.W.T., include: Thick-billed murre (Uria lomvia), Black guillemot (Cepphus grylle), Black-legged kittiwake (Rissa tridactyla), Glaucous gull (Larus hyperboreus), and Northern fulmar (Fulmarus glacialis).

In this study we propose a method for quantifying the energy of stomach contents from these seabird species, and we present preliminary results on the energy contribution of different prey groups to diets of seabirds in the Canadian High Arctic.

Materials and Methods

Seabirds were collected from Barrow Strait and Resolute Passage, near Resolute Bay, Cornwallis Island, N.W.T., during the open water seasons of July-August 1988-90. Stomach samples were obtained from Thick-billed murres (n = 48), Black guillemots (n = 35); Black-legged kittiwakes (n = 30), Glaucous gulls (n=14), and Northern fulmars (n = 42).

Stomach contents were first divided into fish and invertebrate remains. Fish otoliths and cephalopod beaks were removed and stored on glycerin. The remaining content was preserved in 10 % formalin prior to analysis. Invertebrates were sorted into major taxonomic groups and identified (e.g., Sars 1901-1918; Tencati and Leung 1970). Whole specimens were oven dried at 60 °C to constant weight (48 h). Dry weights of identifiable fragments were estimated using regression equations developed by Bradstreet (1980). A correction factor of 1.24 was applied to account for weight changes due to

formalin storage (Giguère et al. 1989). Cephalopods were not included in dry weight estimates since fresh cephalopod were never observed on stomachs and beaks may remain in stomachs for several weeks (Furness et al. 1984).

The glycerin stored otoliths were identified based on shape (Härkönen 1986) and compared to otoliths collected from different Arctic fish species; only a few of the otoliths were from species other than Arctic cod. Maximum length of each otoliths was measured under a dissection microscope. If length could not be measured (broken otoliths) the maximum width was used, and if none of these measurements could be obtained (pieces of otoliths) the otolith was not included. Each otolith pair, right and left otolith, of the same size were assumed to represent one fish. Additional unpaired otoliths were also assumed to represent one fish each.

Arctic cod and invertebrates were collected from the Resolute Bay area in 1988-90. For each taxon, caloric density of dried, homogenized samples (1.0 g) were determined by adiabatic bomb calorimetry (Adiabatic bomb calorimeter 1241) with results expressed in Joules (1 calorie = 4.1855 J).

Results and Discussion

A length-weight relationship was determined for Arctic cod (2-22 cm; Figure A-1a). Otoliths from this size range of fish were measured, and otolith size - fork length relationships were established by regression analysis (Figure A-1b). Based on these relationships and the mean energy content of juvenile and adult Arctic cod (Table A-1), relationships between otolith size and energy content were determined (Figure A-1b) (Table A-1). The total energy value represented by otoliths in each predator stomach were determined by counting and measuring the otoliths and then estimating the energetic contribution by each fish (Figure A-1b). The energy contribution by each invertebrate taxon was determined from its estimated dry weight and energy content (Table A-1).

Arctic cod contributed with 98-100 % of the energy of stomach contents in the five seabird species (Table A-2). Other fish species (zoarcids and cottids) were found in stomachs of Thick-billed murres and Black guillemots, but their energy contribution was small (< 2 %). Overall, invertebrates were about three times as numerous as fish, but their energy contribution was only 0.14 %, because of their small size relative to fish. The total estimated energy of stomach contents in the five seabird species was related to the size of the birds, with the larger species generally having more food in their stomachs.

The amount of otoliths and invertebrates in predator stomachs may be directly related to food intake. According to Jobling and Breiby (1986), otoliths found in stomachs of marine mammals and birds probably represent the remnants of a single feeding bout. They do not seem to accumulate in stomachs and are normally evacuated from the stomachs together with the content; they are subsequently found in faeces of both birds and marine mammals (e.g., Witt et al. 1981; Brown and Mate 1983). Any accumulation of otoliths would result in an overestimate of the number of fish consumed; in contrast, the gastric acid in bird stomachs tend to abrade the otoliths, so that their size represents an underestimate of the size of the fish consumed. We did not control for these biases that work in opposite directions. Similarly, differential digestion of various invertebrates was not accounted for. The gravimetric method is usually believed to over-emphasize the contribution of heavy food items in the diet (Hyslop 1980), and the contribution of small invertebrate species will likely be underestimated. However, given that we were interested in energetic contribution of prey to the diets, we considered this emphasis to be appropriate.

Table A-1. Dry/wet weight ratios (%) and energy content in samples (n) of Arctic cod and invertebrates. Values for juvenile Arctic cod included whole fish (n=15), whereas values for adults (50 males + 50 females) were calculated based on wet weight contributions and respective energy content of samples (n=7) from each of four tissues; carcass, liver, intestine, and gonad. Presented data are means (± SE).

Source	n	Dry/wet weight (%)	Energy content ($kJ \cdot g^{-1}$ dry wt.)	Energy content ($kJ \cdot g^{-1}$ wet wt.)
Arctic cod				
Juveniles	15	21.76±0.31	25.539±0.187	5.557±0.041
Adults	100	24.71±0.15	26.140±0.092	6.459±0.023
Invertebrates				
Calanus	5	31.29±1.48	31.008±0.451	9.702±0.141
Anonyx	3	26.91±1.80	16.095±0.770	4.331±0.207
Parathemisto	6	19.42±1.99	21.086±1.225	4.095±0.238
Onisimus	7	28.57±1.98	22.166±0.506	6.333±0.145
Gammarus	1	29.27	21.517	6.298
Mysis	6	26.32±1.03	24.794±0.282	6.526±0.074
Euphausia	5	21.94±0.16	22.317±0.018	4.896±0.004
Limacina	1	22.76	21.227	4.831

Table A-2. Number and energy of fish and invertebrate prey in stomach contents from five species of seabirds in the Canadian High Arctic, 1988-90. Data are mean values per stomach containing food (n). Number of empty stomachs are indicated (e).

	Thick-billed murre (n = 47, e =1)		Black guillemot (n = 28, e = 7)		Black-legged kittiwake (n = 24, e = 5)		Glaucous gull (n = 12, e = 2)		Northern fulmar (n = 33, e = 9)		Total (n = 144, e =25)	
Prey	Number	Energy (kJ)	Number	Energy (kJ)	Number	Energy (kJ)	Number	Energy (kJ)	Number	Energy (kJ)	Number	Energy (kJ)
Fish:	4.94	537.7	1.22	97.0	2.58	471.1	2.25	715.3	0.88	317.6	11.87	2138.7
Arctic cod	4.83	527.2	1.18	96.6	2.58	471.1	2.25	715.3	0.88	317.6	11.72	2127.8
Other fishes	0.11	10.5	0.04	0.4	0.00	0.0	0.00	0.0	0.00	0.0	0.15	10.9
Invertebrates:	4.70	0.7	5.94	1.1	1.63	0.4	0.00	0.0	18.15	0.8	30.42	3.0
Amphipods	3.17	0.5	4.79	0.7	1.63	0.4	0.00	0.0	1.36	0.3	10.95	1.9
Mysids	1.53	0.2	1.11	0.4	0.00	0.0	0.00	0.0	0.00	0.0	2.64	0.6
Copepods	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	12.94	0.5	12.94	0.5
Cephalopods	0.00	-	0.04	-	0.00	-	0.00	-	3.85	-	3.89	-
Total:	9.64	538.4	7.16	98.1	4.21	471.5	2.25	715.3	19.03	318.4	42.29	2141.7

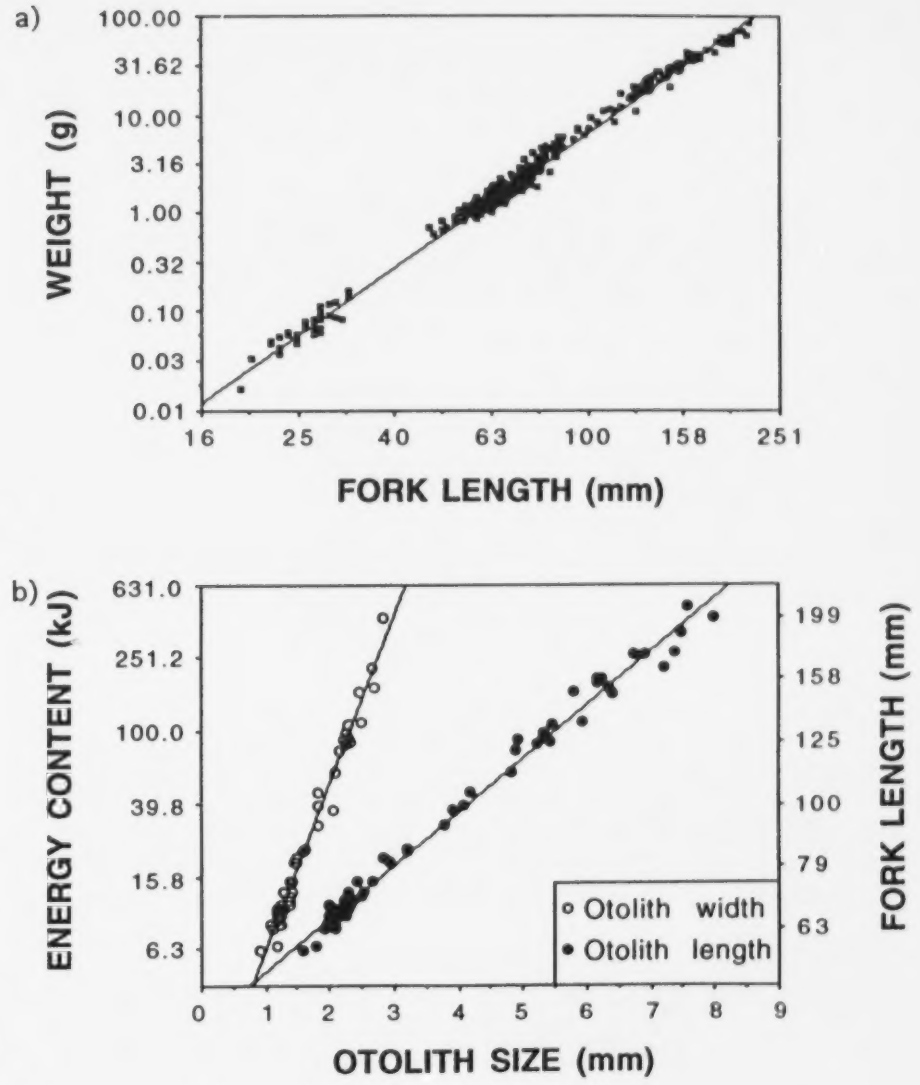

Figure A-1. Relationships between fork length, weight, otolith size and energy for Arctic cod, by regressions ($p = 0.0001$).

a) Relationship between fork length (FL, mm) and total wet weight (WT, g):

$\log WT = 3.42 \log FL - 6.022$, $r^2 = 0.988$.

b) Relationships between otolith size (OL = length, and OW = width, mm) and fork length (FL, mm) or energy content (EC, kJ):

$\log FL = 0.086\ OL + 1.644$, $r^2 = 0.990$; $\log FL = 0.269\ OW + 1.495$, $r^2 = 0.981$.

$\log EC = 0.295\ OL + 0.380$, $r^2 = 0.990$; $\log EC = 0.919\ OW - 0.130$, $r^2 = 0.981$.

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